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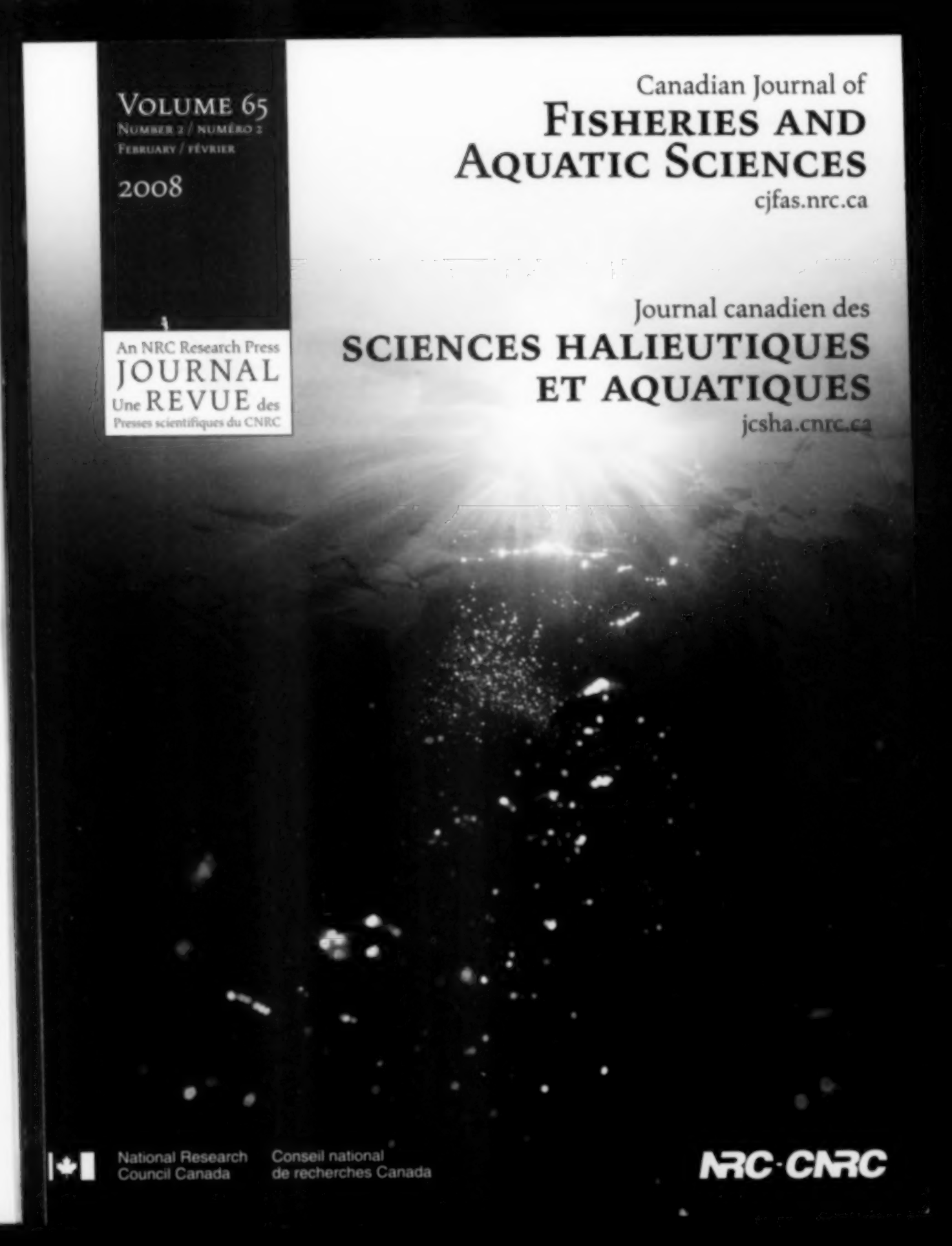

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# Otolith chemistry indicates population structuring by the Antarctic Circumpolar Current

**Julian R. Ashford, Cynthia M. Jones, Eileen E. Hofmann, Inigo Everson, Carlos A. Moreno, Guy Duhamel, and Richard Williams**

**Abstract:** Large-scale transport of seawater in ocean currents may generate spatially complex population structure through the advection of life stages of marine fish species. To test this, we compared the chemistry of otolith nuclei from Patagonian toothfish (*Dissostichus eleginoides*), presently managed as spatially discrete populations corresponding to fishing management areas along the Antarctic Circumpolar Current (ACC), which transports water eastward around the Southern Ocean. The chemistry of otolith nuclei, laid down during early life, differed significantly between fishing areas off South America and the Antarctic and between some Antarctic areas. However, we found significant discrepancies from expectation for a population structure corresponding to fishing areas. We also found evidence of four groups of fish with different early life chemistry: one associated with South America and three Antarctic groups showing mixing consistent with advective transport along the ACC. These results suggest that toothfish populations are structured by their physical environment; population abundance and persistence may rely on a restricted number of breeding members with access to spawning grounds, whereas fisheries may rely substantially on nonbreeding vagrants transported from fishing areas upstream.

**Résumé :** Le transport à grande échelle de l'eau de mer par les courants océaniques peut produire des structures de population complexes par advection des différents stades vitaux des espèces de poissons marins. Pour tester cet énoncé, nous avons comparé la chimie des noyaux des otolithes chez la légine australe (*Dissostichus eleginoides*), une espèce qui est actuellement gérée comme étant formée de populations discontinues dans l'espace et correspondant aux unités de gestion de la pêche le long du courant circumpolaire antarctique (ACC) qui transporte l'eau vers l'est dans l'Océan austral. La chimie des noyaux des otolithes, déterminée tôt dans le cycle biologique, diffère significativement dans les zones de pêche au large de l'Amérique du Sud et dans celles de l'Antarctique, ainsi que dans certaines zones de l'Antarctique. Nous trouvons cependant d'importantes discordances par rapport à la structure de population à laquelle on pourrait s'attendre si celle-ci était reliée aux zones de pêche; il y a des indications de l'existence de quatre groupes de poissons avec une chimie différente au cours des premiers stades, un associé à l'Amérique du Sud et trois groupes antarctiques qui présentent des mélanges compatibles avec le transport advectif le long de ACC. Ces résultats indiquent que les populations de légines sont structurées par leur environnement physique; l'abondance et la persistance des populations doit peut-être alors dépendre d'un petit nombre de reproducteurs qui ont accès aux lieux de reproduction, alors que la pêche dépend de manière importante de poissons errants non reproducteurs qui sont transportés dans le courant à partir des zones de pêche.

[Traduit par la Rédaction]

## Introduction

### Population structure and advection

Managers of oceanic fisheries frequently rely on stock assessment models that assume a randomly mixing, closed population delineated by barriers that curtail exchange with neighbouring populations. Physical barriers cited include deep water and oceanic fronts (e.g., Kingsford 1993; Loeb et al. 1993). Yet fronts are often associated with fast-moving currents capable of transporting fish between habitats and across deep water. Where these currents result in movement to incompatible habitat, life stages are lost to the source population through advective mortality. Where currents connect to appropriate habitat, advection can structure marine popu-

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lations in spatially complex ways (e.g., Harden Jones 1968; Cushing 1981), promoting overlapping distributions of older stages that were nevertheless spawned on separate grounds.

Advection can connect these different populations genetically if transported fish remain to breed in their new area rather than returning to where they were spawned. This connectivity can be important to the persistence of populations; migration from source populations, where high recruitment relative to mortality allows emigration, can maintain sink populations, where low recruitment relative to mortality may otherwise lead to extinction (Pulliam 1988; Polachek 1990). If harvest interrupts the supply of migrants by source populations, it will reduce abundance over an extended area.

Even when advected fish do not breed or return to their original population, they can remain as nonbreeding vagrants (Sinclair 1988; Sinclair and Iles 1989). Population persistence may then depend on only those fish that have access to their spawning grounds, whose fecundity and rate of survival is capable of offsetting the loss of vagrants through advection. If so, harvest of these breeding members can interrupt the supply of vagrants, like the harvest of source populations supplying migrants, with a disproportionate impact on abundance over a wide area.

To examine population structure, researchers have used approaches such as artificial tags, population vital rates, and genetics (e.g., Ihssen et al. 1981). Although these approaches are generally efficient at testing whether fish are from a single panmictic population or not, they are less effective in telling whether spatial heterogeneity is due to discrete, closed populations or spatially complex structure, where fish come from more than one population. Success in assigning individual fish to a population using hyper-variable genetic markers nevertheless requires that the underlying populations have been identified and the multilocus genotypes of a representative sample are known (e.g., Cornuet et al. 1999). A more recent approach in oceanic fisheries is the use of natural chemical markers in otoliths, which show characteristic properties related to the environment to which fish are exposed (e.g., Edmonds et al. 1991). Growth increments in otoliths, used for aging fish, provide a chronology covering the life history to capture. One consequence is that the chemistry of otolith nuclei, laid down during early life, can be used to detect early spatial separation resulting from segregation during spawning (e.g., Campana et al. 1994) and hence population structure.

## Physical structuring of populations in the Southern Ocean

The Polar Front (PF), one of several within the Antarctic Circumpolar Current (ACC), separates regions around South America and the Antarctic into different hydrographic regimes, and frontal currents may disperse life stages into deep water away from suitable habitat (e.g., Rogers et al. 2006). Recently, genetic data indicated a sharp population boundary in the vicinity of the PF between Patagonian toothfish (*Dissostichus eleginoides*) along the Patagonian Shelf and around South Georgia in the Southwest Atlantic (Fig. 1) (Shaw et al. 2004), corroborating evidence from length-at-age data (Ashford 2001).

Yet the ACC also connects the major southern hemisphere continents and islands and banks around the Antarctic and may promote ecologically important linkages (Hofmann and Murphy 2004). There is strong evidence that another front in the ACC, the Southern ACC Front, transports Antarctic krill (*Euphausia superba*) from the western Antarctic Peninsula and southern Scotia Sea to supply nonbreeding stocks off South Georgia on a time scale of 2–12 months (Hofmann et al. 1998; Murphy et al. 2004; Fach et al. 2006). Fronts in the ACC penetrate the entire water column (e.g., Nowlin and Clifford 1982) and are identifiable around the Antarctic (Hofmann 1985; Orsi et al. 1995) associated with biological production due to upwelling. Under these conditions, marine organisms dispersed by frontal currents may survive, like krill from the Antarctic Peninsula, to be advected to appropriate habitat downstream, structuring populations in spatially complex ways.

## Population connectivity and Patagonian toothfish

In contrast with krill, the otoliths in marine fish provide a way to test directly for physical structuring of populations. Recently, chemistry in the otolith nuclei of toothfish have detected the population division between the Patagonian Shelf and South Georgia (Ashford et al. 2006; Ashford and Jones 2007). Toothfish are managed off South America within national Exclusive Economic Zones (EEZs) and in the Antarctic by the Commission of the Convention for the Conservation of Antarctic Marine Living Resources (CCAMLR) as spatially discrete stocks corresponding to fishing areas around islands and seamounts. This assumes no movement between fishing areas, yet available data indicate young stages of toothfish are pelagic (North 2002), and mature adults are inferred to be neutrally buoyant (Oyarzun 1988; Eastman 1993), considerably reducing the energetic cost of dispersal. They live up to 50+ years (Ashford 2001; Horn 2002), substantially longer than krill, and have been recaptured far from where they were tagged (e.g., Williams et al. 2002) or spawned (Moller et al. 2003).

Moreover, age-at-length frequencies, while varying between the Falkland Islands and South Georgia, showed no differences between South Georgia and Kerguelen Island downstream (Ashford 2001). These data suggest that the ACC provides opportunities to move along the current with little energetic cost, but constrains movement in other directions (Ashford et al. 2003). Evidence from genetic studies is mixed: (*i*) little heterogeneity between South Georgia and some habitats downstream, but differentiation with others (Rogers et al. 2006); (*ii*) little differentiation between Prince Edward Island in the Indian Ocean and Crozet and Kerguelen islands further downstream (Appleyard et al. 2004), but heterogeneity among Heard Island on the Kerguelen Plateau, Macquarie Island in the Pacific Ocean, and South Georgia (Appleyard et al. 2002).

These results may be explained by spatially complex population structure, with heterogeneity resulting from fish mixing in different frequencies from more than one population. Similarities, on the other hand, may result from low levels of gene flow between populations that homogenize differences, rendering genetic markers incapable of distinguishing population structure. Otolith chemistry, in contrast, takes advan-

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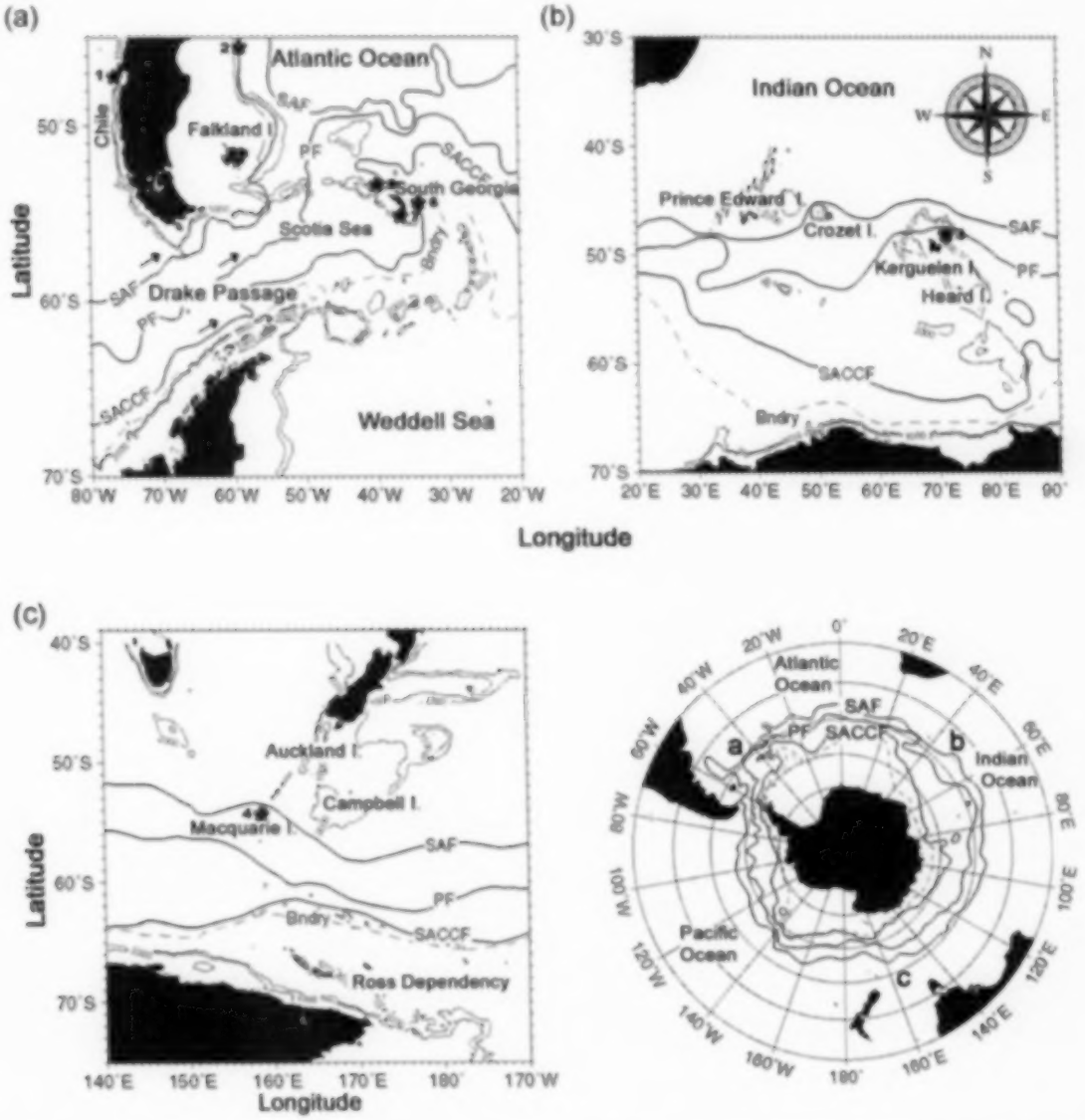
**Fig. 1.** Detailed maps of the (*a*) Atlantic, (*b*) Indian, and (*c*) Pacific sectors of the Southern Ocean, showing mean position of major fronts and sampling areas. SAF, Subantarctic Front; PF, Polar Front; SACCF, southern Antarctic Circumpolar Current Front, southern boundary of the ACC is shown as a broken line (Orsi et al. 1995). Arrows show current direction. Sampling areas: 1, Chile 1996; 2, Falkland Islands 1997; 3, Kerguelen Island 1996; 4, Macquarie Island 1996; 5, South Georgia 1996; 6, South Georgia 1997; 7, South Georgia 1998.




tage of biogeochemical variation generated by oceanic environments (e.g., Ashford et al. 2005; Ashford and Jones 2007). Where populations are discrete and exposed to different environments, the chemistry of otolith nuclei can be expected to diverge strongly, reflecting early life separation. But where fish subsequently mix, the nuclei will show distributions corresponding to the early life exposures of the component populations.

Otolith nuclei have already suggested population heterogeneity in toothfish off the Patagonian Shelf, which was not detected by genetic approaches (Ashford et al. 2006). In this study, therefore, we used nucleus chemistry to test whether toothfish are distributed in spatially discrete, closed populations that correspond to fishing areas or in a more complex structure resulting from advection along the ACC, in which sampling areas show mixing with fish carrying similar early life chemistry to those upstream. Sampling around the Southern Ocean and along the eastern boundary of the southern Pacific Ocean and western boundary of the southern Atlantic Ocean, we undertook the first integrated study

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linking nucleus chemistry with the physical structuring of populations across the range of an oceanic species.

## Materials and methods

### Otolith analysis procedures

Otoliths were collected between March and April 1996 from commercial catches of Patagonian toothfish off the northern continental slope of South Georgia (United Nations Food and Agriculture Organization Statistical Sub-Area 48.3); off the eastern continental slope of Kerguelen (Division 58.5.1); and off the west coast of the Macquarie Island EEZ (Fig. 1). Details of otolith collection are found in Ashford et al. (2005), and a brief summary is given here. For the region around South America, observers sampled fish from artesanal fishermen returning to Chiloe Island in the Chilean national EEZ. Between April and May 1997, observers collected a second set of samples off the slope of the Patagonian Shelf northeast of the Falkland Islands Conservation Zone (FCZ) and off the eastern slope of South Georgia. At each collection, observers sampled female toothfish between 90 and 110 cm to minimize effects due to sex and life stage. Off Chile, otoliths could not be collected before removal of gonads by fishermen, and sex data were not recorded. We also selected otoliths randomly from observer sample sets taken in 1998 off the southern shelf slope of South Georgia. All samples were taken from depths greater than 1000 m, except at Macquarie Island, where the depths were ~400–500 m.

Otoliths were dried and stored in envelopes and returned to the laboratory at Old Dominion University, Norfolk, Virginia, USA. Preparation of otoliths for elemental analysis is outlined in Ashford et al. (2005). We used a Finnegan Mat Element 2 double-focusing sector-field inductively coupled plasma mass spectrometer (ICP-MS) located at the Laboratory for Isotope and Trace Element Research (LITER) at Old Dominion University to examine otoliths for minor and trace element chemistry. Instrument details are given in Jones and Chen (2003). Samples were introduced in automated sequence (Chen et al. 2000) using a New Wave Research EO LUV 266 laser ablation system and a PFA microflow nebulizer. Ablated otolith material from the sample cell was mixed in the spray chamber with aerosol of 1% $HNO_3$ introduced by the nebulizer, and the mixture was then carried to the ICP torch. Laboratory calibration standards consisted of known-concentration, multi-element solutions synthesized from stock single element standards and were similarly introduced to the spray chamber by the nebulizer as an aerosol before being carried to the ICP torch. Blanks of 1% $HNO_3$ aerosol also were introduced to the chamber by the nebulizer.

For quality control, we used dissolved otolith reference material obtained from the National Research Council of Canada. To control for operational variability in the laser–ICP-MS, a randomized blocks design was used with each petrographic slide as the blocking factor, considered randomly drawn, with each sampling area considered a fixed treatment. Blank and standard readings of count rate (counts·s$^{-1}$) were obtained before and after random presentation of the otolith sections in each block. Readings of reference material were obtained before sample presentation.

Otoliths were analysed for $^{48}$Ca, $^{25}$Mg, $^{55}$Mn, $^{88}$Sr, and $^{138}$Ba and reported as ratios to $^{48}$Ca. To calculate element:Ca (Me·Ca$^{-1}$) ratios, background counts were subtracted from otolith counts by interpolating between readings taken before and after each block of otoliths, and the corrected otolith counts were converted to Me·Ca$^{-1}$ concentrations using the standards. To sample the nucleus, we used a grid raster type 200 µm × 200 µm with a laser beam of diameter 20 µm traveling at 6 µm·s$^{-1}$, set at 60% power and frequency at 10 Hz, giving a predicted crater depth of approximately 100 µm (Jones and Chen 2003, eq. 3). Dwell time was 15.0 ms.

### Statistical methods

A spatially discrete population structure that corresponds to fishing areas implies fish in each area were spawned separately from those in other areas and therefore were exposed to different early life environments. This in turn would be recorded in their otolith chemistry. To test for these differences, we applied analysis of variance (ANOVA), using separate univariate analyses to examine the behaviour of each element ratio. Multivariate outliers were identified by plotting robust squared Mahalanobis distances of the residuals ($D_i^2$) against the corresponding quantiles (Q–Q plot) of the $\chi^2$ distribution.

The assumption of multivariate normality was checked analytically using tests ($\alpha = 0.05$) based on Mardia's multivariate skewness and kurtosis measures (Khattree and Naik 1999) and graphically using Q–Q plots of squared Mahalanobis distances ($d_i^2$). Data distributions were not normal, showing long tails instead. We used variance-stabilizing transformations from the ladder of powers (Kuehl 1994; Ashford et al. 2007), which also fulfilled the assumption of multivariate normality. The data transformations selected were $y^{-0.2}$ for Mg·Ca$^{-1}$, $y^{0.25}$ for Mn·Ca$^{-1}$, $y^{0.8}$ for Sr·Ca$^{-1}$, and $y^{-0.5}$ for Ba·Ca$^{-1}$, which reduced the tails of the distributions in a similar way to standard lognormal transformations.

Because variance–covariance matrices were not equal according to Bartlett's modification ($\chi^2 = 96.7$, df = 60, $p > \chi^2 = 0.0019$), multivariate ANOVA was inappropriate, and we used univariate ANOVA for each Me·Ca$^{-1}$ ratio instead. Residuals for each treatment were normally distributed (Kolmogorov–Smirnov test; $\alpha = 0.05$), except for fish taken off Chile for Mg·Ca$^{-1}$ only (Kolmogorov–Smirnov test; $p = 0.034$). All Me·Ca$^{-1}$ ratios showed equality of variances ($F_{max}$ test; $t = 7$, $v = 17$; $\alpha = 0.01$). As a result, we used ANOVA to test between sampling areas separately for each trace element measured, with Student–Newman–Keuls (SNK) multiple range tests for pairwise comparisons between sampling areas, adjusted for an experiment-wise $\alpha = 0.0125$. We calculated power $1 - \beta$ in an a posteriori manner separately for each ANOVA test (Sokal and Rohlf 1995) and found $1 - \beta > 0.99$ for all four elements.

Spatial heterogeneity can also result when fish, though spawned separately, then disperse and mix in different proportions between sampling areas. Therefore, to examine whether spatial heterogeneity was due to discrete populations or mixing of more than one, we examined the data from individual fish graphically using nonmetric multidimensional scaling (NMDS) (Kruskal and Wish 1978; Schiffman et al. 1981). Because the variables had different absolute magnitudes and

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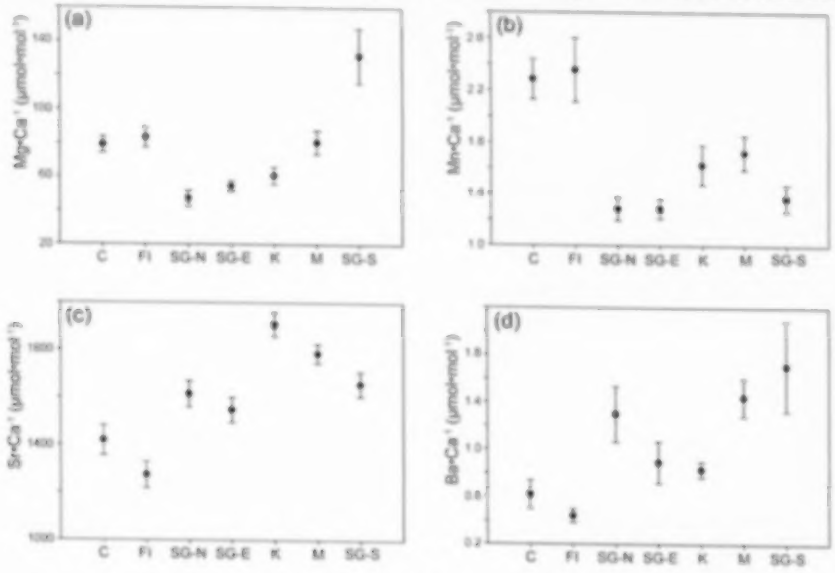
**Fig. 2.** Elemental ratio ($Me\text{-}Ca^{-1}$) concentrations found in the nuclei of otoliths from Patagonian toothfish (*Dissostichus eleginoides*) captured at sampling areas in the Southern Ocean between 1996 and 1997. Bars show standard error. C, Chile; FI, Falkland Islands; SG-N, north South Georgia; SG-E, east South Georgia; K, Kerguelen Island; M, Macquarie Island; SG-S, south South Georgia.




ranges, they were standardized to the same scale. Constructing a dissimilarity matrix based on Euclidean distances, we created a two-dimensional projection of distance between individual fish using a convergence criterion of Stress < 0.01. We also employed cluster analysis to detect fish crossing between sampling areas using Ward's minimum variance hierarchical approach on the standardized data. To determine the quality of clustering, we used root mean square standard deviation, semipartial $R^2$, $R^2$, and between-cluster sum of squares to measure the loss of homogeneity through successive merging of clusters. The appropriate number of clusters was taken as that below which the measures began to change markedly (Khattree and Naik 2000).

## Results

Otolith nucleus chemistry showed significant heterogeneity between samples from South American and Antarctic fishing areas (Fig. 2, Tables 1–4). Samples taken from the Chilean EEZ and north of the FCZ showed similar concentrations of all four element ratios, but both showed concentrations of $Mg\text{-}Ca^{-1}$ ($\bar{y}_C$ = 79.3 μmol·mol$^{-1}$; $\bar{y}_{FI}$ = 83.6 μmol·mol$^{-1}$) that were significantly higher than samples taken from north and east of South Georgia ($\bar{y}_{SGn}$ = 47.2 μmol·mol$^{-1}$; $\bar{y}_{SGe}$ = 54.6 μmol·mol$^{-1}$) and significantly lower than the sample taken from south of South Georgia ($\bar{y}_{SGs}$ = 131.9 μmol·mol$^{-1}$). Mean concentrations of $Mn\text{-}Ca^{-1}$ off Chile ($\bar{y}_C$ = 2.29 μmol·mol$^{-1}$) and the FCZ ($\bar{y}_{FI}$ = 2.36 μmol·mol$^{-1}$) were higher than all Antarctic areas, significantly so for Kerguelen and all South Georgia samples (ranging from $\bar{y}_{SGe}$ = 1.28 μmol·mol$^{-1}$ to $\bar{y}_K$ = 1.63 μmol·mol$^{-1}$). On the other hand, mean concentrations of $Sr\text{-}Ca^{-1}$ off Chile ($\bar{y}_C$ = 1419.8 μmol·mol$^{-1}$) and the FCZ ($\bar{y}_{FI}$ = 1274.7 μmol·mol$^{-1}$) were lower than those in all Antarctic areas, significantly so for Kerguelen, Macquarie, and south of South Georgia (ranging from $\bar{y}_{SGs}$ = 1657.1 μmol·mol$^{-1}$ to $\bar{y}_K$ = 1907.6 μmol·mol$^{-1}$). Mean concentrations of $Ba\text{-}Ca^{-1}$ off Chile ($\bar{y}_C$ = 0.62 μmol·mol$^{-1}$) and the FCZ ($\bar{y}_{FI}$ = 0.44 μmol·mol$^{-1}$) were also significantly lower than those in all Antarctic areas (ranging from $\bar{y}_K$ = 0.83 μmol·mol$^{-1}$ to $\bar{y}_{SGs}$ = 1.71 μmol·mol$^{-1}$).

Consistent with spatially discrete populations corresponding to fishing areas, the otolith nuclei showed further heterogeneity between samples from fishing areas within the Antarctic. Kerguelen and Macquarie had $Mg\text{-}Ca^{-1}$ concentrations ($\bar{y}_K$ = 60.1 μmol·mol$^{-1}$; $\bar{y}_M$ = 80.9 μmol·mol$^{-1}$) that were significantly higher than samples from north and east of South Georgia and significantly lower than those south of South Georgia. Kerguelen also showed significantly higher concentrations of $Sr\text{-}Ca^{-1}$ than all South Georgia samples (ranging from $\bar{y}_{SGe}$ = 1547.5 μmol·mol$^{-1}$ to $\bar{y}_{SGs}$ = 1657.1 μmol·mol$^{-1}$); Macquarie showed mean concentrations of $Sr\text{-}Ca^{-1}$ ($\bar{y}_M$ = 1785.9 μmol·mol$^{-1}$) that were higher than all South Georgia samples, significantly so compared with east of South Georgia.

However, mean $Me\text{-}Ca^{-1}$ concentrations showed major discrepancies from expectation for a population structure corresponding to fishing areas. Despite coming from the respective eastern and western boundaries of separate ocean systems around South America, mean concentrations of samples taken from fishing areas off Chile and the FCZ showed no significant difference (Fig. 2, Tables 1–4). Similarly in the Antarctic, ANOVA detected no heterogeneity between samples taken from fishing areas around Kerguelen and Macquarie. In contrast, within a single fishing area off South Georgia, samples were significantly different; the sample taken south of the island had significantly higher $Mg\text{-}Ca^{-1}$ concentrations than those taken to the north and east.

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**Table 1.** Results from analysis of variance (ANOVA) and Student–Newman–Keuls tests of $Mg{\cdot}Ca^{-1}$, showing differences in concentrations measured in the otolith nuclei of Patagonian toothfish (*Dissostichus eleginoides*) between sampling areas off South America and in the Antarctic.

| | *df* | SS | MS | *F* | *p* |
|---|---|---|---|---|---|
| Sample | 6 | 0.0765 | 0.0127 | 16.38 | <0.0001 |
| Error | 123 | 0.0957 | 0.0008 | | |
| Total | 129 | 0.1722 | | | |

| SG-S | FI | C | M | K | SG-E | SG-N |
|---|---|---|---|---|---|---|
| Area | C | FI | SG-N | SG-E | SG-S | K |
| FI | NS | | | | | |
| SG-N | + | + | | | | |
| SG-E | + | + | NS | | | |
| SG-S | + | + | + | + | | |
| K | NS | NS | NS | NS | + | |
| M | NS | NS | + | + | + | NS |

**Note:** Lines denote no significant difference; NS, no significant difference; +, significant difference ($\alpha = 0.05$); C, southern Chile ($n = 19$); FI, Falkland Islands ($n = 19$); SG-N, north of South Georgia ($n = 17$); SG-E, east of South Georgia ($n = 17$); K, Kerguelen Island ($n = 20$); M, Macquarie Island ($n = 20$); SG-S, south of South Georgia ($n = 17$).

**Table 2.** Results from analysis of variance (ANOVA) and Student–Newman–Keuls tests of $Mn{\cdot}Ca^{-1}$, showing differences in concentrations measured in the otolith nuclei of Patagonian toothfish (*Dissostichus eleginoides*) between sampling areas off South America and in the Antarctic.

| | *df* | SS | MS | *F* | *p* |
|---|---|---|---|---|---|
| Sample | 6 | 0.5614 | 0.0936 | 9.57 | <0.0001 |
| Error | 123 | 1.2020 | 0.0098 | | |
| Total | 129 | 1.7634 | | | |

| SG-N | SG-E | SG-S | K | M | FI | C |
|---|---|---|---|---|---|---|
| Area | C | FI | SG-N | SG-E | SG-S | K |
| FI | NS | | | | | |
| SG-N | + | + | | | | |
| SG-E | + | + | NS | | | |
| SG-S | + | + | NS | NS | | |
| K | + | + | NS | NS | NS | |
| M | NS | NS | NS | NS | NS | NS |

**Note:** Refer to Table 1 for explanation of lines and definitions.

Examining the distribution of data graphically, multidimensional scaling corroborated the strong separation between the FCZ and both western and eastern South Georgia sampling areas (Stress = 0.14; Fig. 3*a*). All three areas showed strong separation from southern South Georgia, which, although it included some fish similar to those taken north and east of the island, showed most fish to have a very different nucleus chemistry that implied a separate early life history. On the other hand, like the samples from western and eastern South Georgia, fish from west and east of South America showed similar nucleus chemistry distributions (Fig. 3*b*), indicating similar early life histories. Downstream of South Georgia along the ACC, samples from Kerguelen included fish similar to those taken north and east of South Georgia, but also included others with very different nucleus chemistry (Fig. 3*c*). Moreover, the nucleus chemistry distribution of these Kerguelen-caught fish was similar to that of those caught at Macquarie Island, and both showed similarities to fish taken from south of South Georgia.

Examining this further, cluster analysis indicated that the distributions detected using NMDS resolved most appropriately into four clusters (Table 5, Figs. 4*a*, 4*b*); the statistical measures changed sharply when reducing to three clusters. Lower concentrations of $Sr{\cdot}Ca^{-1}$ and $Ba{\cdot}Ca^{-1}$ and higher

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**Table 3.** Results from analysis of variance (ANOVA) and Student–Newman–Keuls tests of $Sr{\cdot}Ca^{-1}$, showing differences in concentrations measured in the otolith nuclei of Patagonian toothfish (*Dissostichus eleginoides*) between sampling areas off South America and in the Antarctic.

| | df | SS | MS | *F* | *p* |
|---|---|---|---|---|---|
| Sample | 6 | 184 140 | 30 690 | 17.41 | <0.0001 |
| Error | 123 | 216 839 | 1 763 | | |
| Total | 129 | 400 979 | | | |

| Fl | C | SG-E | SG-N | SG-S | M | K |
|---|---|---|---|---|---|---|
| Area | C | Fl | SG-N | SG-E | SG-S | K |
| Fl | NS | | | | | |
| SG-N | NS | + | | | | |
| SG-E | NS | + | NS | | | |
| SG-S | + | + | NS | NS | | |
| K | + | + | + | + | + | |
| M | + | + | NS | + | NS | NS |

**Note:** Refer to Table 1 for explanation of lines and definitions.

**Table 4.** Results from analysis of variance (ANOVA) and Student–Newman–Keuls tests of $Ba{\cdot}Ca^{-1}$, showing differences in concentrations measured in the otolith nuclei of Patagonian toothfish (*Dissostichus eleginoides*) between sampling areas off South America and in the Antarctic.

| | df | SS | MS | *F* | *p* |
|---|---|---|---|---|---|
| Sample | 6 | 8.871 | 1.479 | 15.8 | <0.0001 |
| Error | 123 | 11.512 | 0.094 | | |
| Total | 129 | 20.383 | | | |

| M | SG-S | SG-N | K | SG-E | C | Fl |
|---|---|---|---|---|---|---|
| Area | C | Fl | SG-N | SG-E | SG-S | K |
| Fl | NS | | | | | |
| SG-N | + | + | | | | |
| SG-E | + | + | NS | | | |
| SG-S | + | + | NS | NS | | |
| K | + | + | NS | NS | NS | |
| M | + | + | NS | NS | NS | NS |

**Note:** Refer to Table 1 for explanation of lines and definitions.

concentrations of $Mn{\cdot}Ca^{-1}$ separated cluster 1 fish ($n$ = 38) from cluster 2 ($n$ = 52) and cluster 3 ($n$ = 24) fish; whereas $Mn{\cdot}Ca^{-1}$ and $Sr{\cdot}Ca^{-1}$ separated cluster 2 fish from cluster 3 fish. $Mg{\cdot}Ca^{-1}$ and $Mn{\cdot}Ca^{-1}$ separated cluster 4 fish ($n$ = 16) from the other clusters. Cluster 1 fish were mostly caught off South America (79%). The other three clusters were associated mostly with fish taken at sampling sites in the Antarctic (90% of cluster 2 fish; 83% of cluster 3 fish; 100% of cluster 4 fish). As indicated by multidimensional scaling, the percentage of fish from each cluster changed between Antarctic sampling areas. Off the north and east of South Georgia, almost all fish from Antarctic-associated clusters were from cluster 2 (93%), whereas downstream at Kerguelen, 58% were from cluster 2 and the rest from cluster 3. Further downstream still, off Macquarie Island, cluster 2 made up only 26% of the sample, and clusters 3 and 4 made up 53% and 21%, respectively, of the sample. Off the south of South Georgia, 73% of fish from Antarctic-associated clusters were from cluster 4.

## Discussion

### Otolith chemistry and toothfish population structure

The chemistry of otolith nuclei strongly suggested that toothfish population structure is considerably more complex than a series of spatially discrete populations corresponding to fishing areas. Samples taken off South America were very different from those caught in the Antarctic, independently

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**Fig. 3.** Relationships between individual Patagonian toothfish (*Dissostichus eleginoides*) taken from sampling areas in the Southern Ocean, using nonmetric multidimensional scaling (NMDS) based on Euclidean distances. Stress = 0.14. (*a*) Falkland Islands (□); north South Georgia (▲); east South Georgia (△); south South Georgia (+); (*b*) Chile (○), using Falkland Islands and north South Georgia as references; (*c*) Kerguelen (○) and Macquarie (×) islands, using north South Georgia as a reference.

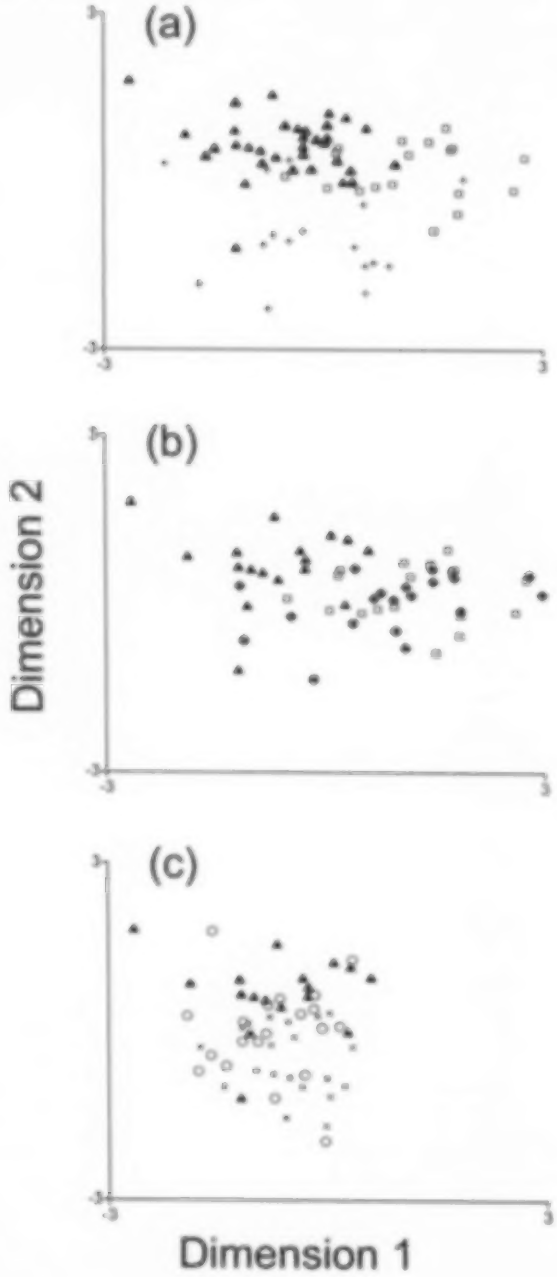
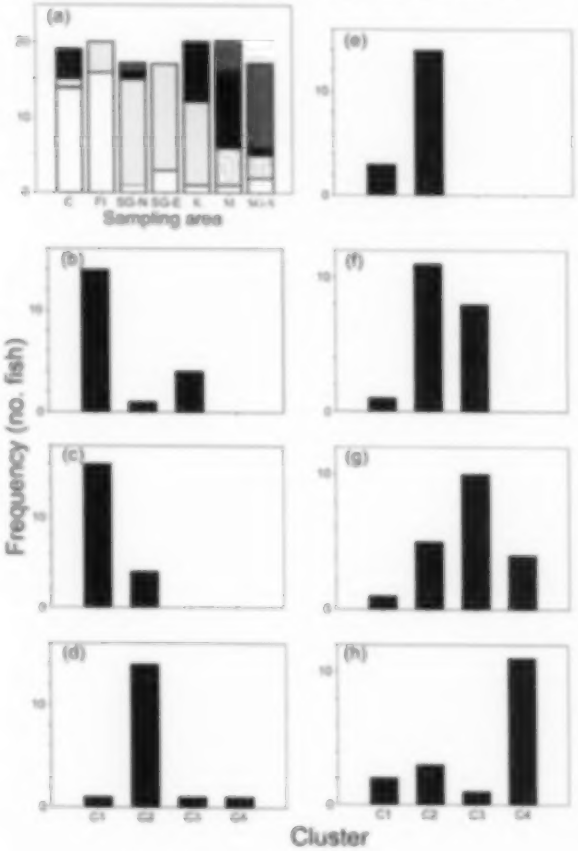



**Table 5.** Summary of statistics measuring quality of clustering.

| Cluster No. | RMSSTD | Semipartial $R^2$ | $R^2$ | BSS |
|---|---|---|---|---|
| 6 | 0.645 | 0.028 | 0.656 | 14.6 |
| 5 | 0.650 | 0.037 | 0.619 | 19.3 |
| 4 | 0.731 | 0.057 | 0.562 | 29.3 |
| 3 | 0.843 | 0.097 | 0.465 | 50.1 |
| 2 | 0.857 | 0.136 | 0.329 | 70.2 |
| 1 | 1.000 | 0.329 | 0.000 | 169.6 |

**Note:** RMSSTD, root mean square standard deviation; BSS, between sum-of-squares. Gap in table shows marked change in measures, indicating an appropriate number of four clusters. Data is from cluster analysis using Ward's minimum variance approach for standardized trace element ratio concentrations measured in the nuclei of Patagonian toothfish (*Dissostichus eleginoides*) captured across the Southern Ocean.

**Fig. 4.** Allocation of Patagonian toothfish (*Dissostichus eleginoides*) captured at sampling areas in the Southern Ocean to four clusters (C1–C4) based on early life history similarities recorded in the chemistry of otolith nuclei. Cluster analysis is based on Ward's minimum variance approach. (*a*) Composite bar chart showing all data; and individual bar charts for (*b*) Chile (C), (*c*) Falkland Islands (FI); (*d*) north South Georgia (SG-N); (*e*) east South Georgia (SG-E); (*f*) Kerguelen Island (K); (*g*) Macquarie Island (M); (*h*) south South Georgia (SG-S).

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corroborating earlier results showing population isolation between fishing areas off the Patagonian Shelf and South Georgia (e.g., Shaw et al. 2004; Ashford et al. 2006; Rogers et al. 2006). However, in the first comparison between toothfish on either side of South America, we found no evidence of segregation during early life that would be consistent with spatially discrete populations; nucleus chemistry strongly suggested that toothfish had the same population structure. In contrast, at South Georgia, fish caught south of the island showed nucleus chemistry that was significantly different from those taken to the north and east, suggesting population heterogeneity within a single fishing area in the ACC.

The north and east South Georgia samples were also different from those taken downstream along the ACC, at Kerguelen and Macquarie islands, consistent with previous genetic data (Appleyard et al. 2002), although in contrast with the genetic data, ANOVA showed little heterogeneity between Kerguelen and Macquarie islands. Unlike genetic approaches, however, which rely on discriminating genetic frequencies between sampling areas, otolith chemistry data are highly amenable to techniques capable of detecting grouping within and across samples. These analyses suggested two groups of fish mixing at Kerguelen, one of which had similar early life distributions to north and east South Georgia and the other to Macquarie Island. The analyses also suggested that there was indeed heterogeneity between Kerguelen and Macquarie islands, but that this was due to the proportions of fish mixing from the same two groups, as well as fish from a third group that were present at Macquarie and not at Kerguelen. This third group showed considerable similarity to fish found off southern South Georgia.

### Otolith chemistry and hydrography

Otolith chemistry has successfully discriminated spatial heterogeneity in several exclusively marine fish species (e.g., Edmonds et al. 1991; Campana et al. 1994). Validations for Patagonian toothfish demonstrated that the characteristic spatial properties of otolith markers resulted in correct allocation of fish to South American and Antarctic regions (Ashford et al. 2005; Ashford and Jones 2007). The chemistry of otolith edges, laid down immediately prior to capture, suggested that the distribution of otolith $Sr\text{-}Ca^{-1}$ is related to temperature (Ashford et al. 2005), which in turn distinguishes Circumpolar Deep Water, the largest water mass by volume transported by the ACC (Sievers and Nowlin 1984), from Antarctic Intermediate Water, formed to the north of the PF primarily in the southwest Atlantic (Molinelli 1981; Sievers and Nowlin 1984). Concentrations of $Ba\text{-}Ca^{-1}$ were associated with new production in the open ocean fueled by nitrate (Dehairs et al. 1992), as opposed to recycled nitrogen off continental shelves such as around South America. On the other hand, authigenic activity, particularly along the Patagonian Shelf, and resuspension from anoxic sediments (e.g., Bucciarelli et al. 2001) may explain enrichment of otolith $Mn\text{-}Ca^{-1}$, whereas physiology most likely accounts for otolith $Mg\text{-}Ca^{-1}$ distributions (Ashford et al. 2005, 2006).

Comparing fish from the Patagonian Shelf and the ACC in the Antarctic takes full advantage of the spatial properties of each of these markers. In the nucleus chemistry, all four showed strong contrasts between fish caught off South America and in the Antarctic, on either side of a recognized population boundary, which corroborated earlier results (Ashford et al. 2006). Earlier results also showed that environmental conditions diverged on either side of South America sufficiently to allocate fish with 79%–84% success using chemistry from their otolith edges (Ashford et al. 2005); even so, we found no evidence of early life segregation.

Despite lying downstream of one another, and therefore receiving similar water after a time lag for transport, fish from South Georgia and Kerguelen and Macquarie islands were correctly classified to sampling area at rates of between 50% and 67%, compared with an expected 14% by chance alone. Strong contrasts from our results in the nucleus chemistry around South Georgia and between fish off north and east South Georgia and particularly Macquarie imply that spatial heterogeneity may be more strongly defined during early life because of the restricted area of spawning aggregations and the constrained spatial scales at which young stages can move actively. The quality of clustering changed sharply when reducing from four to three clusters, consistent with strong spatial contrasts experienced by the four groups of fish. Indeed, there was some evidence that the South American-associated cluster contained a further division, supported by prior evidence of two mixing South American populations (Ashford et al. 2006). However, the two groups would have accounted for considerably less variation than the Antarctic-associated clusters.

This heterogeneity is driven by physical and biogeochemical processes that continue within seawater during transport. Water continues to mix, substantially changing the biogeochemical properties of water around the ACC (Kroopnick 1985; Meredith et al. 1999*a*, 1999*b*). The physical structure of the ACC exerts a dominant control on biogeochemical distributions in the Southern Ocean (Pollard et al. 2002). As a consequence, the chemistry recorded in an otolith reflects association with different water masses, zones, and fronts along the ACC, often at quite fine scales. Water, not food, contributes the majority of strontium and barium deposited in the otoliths of marine fish (Walther and Thorrold 2006), and recent evidence shows that edge chemistry distinguished areas downstream of each other along the Patagonian Shelf, separating with 68%–81% success at spatial scales down to 200 nm (Ashford et al. 2007).

### Are populations structured by the ACC?

Such lines of evidence strongly suggest that physical and biogeochemical heterogeneity generate strong early life contrasts not only across frontal systems but also between sampling areas connected by hydrographic transport. Most tellingly, otolith chemistry corroborated heterogeneity where it was previously found by genetic approaches (Smith and McVeagh 2000; Appleyard et al. 2002; Shaw et al. 2004). But it went further, allowing us to directly examine data for evidence of population mixing between Antarctic sampling areas that can be explained by physical structuring through the ACC.

Thus, the Subantarctic Front (SAF), the northern-most of the ACC fronts, flows northwards across the North Scotia Ridge and along the continental shelf off the Falkland Islands through an area noted for mesoscale eddy activity,

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looping south and eastward. The PF turns eastward soon after flowing north across the Scotia Ridge (Meredith et al. 1999*a*; Arhan et al. 2002), and both fronts miss South Georgia. As a consequence, marine organisms from the Falkland Islands EEZ entrained in the northward-flowing SAF would be advected back over the continental shelf. Any remaining in the SAF or PF would be transported downstream without encountering South Georgia, providing a physical segregating mechanism between South America and the Antarctic, but promoting movement along the ACC (Ashford et al. 2003; Rogers et al. 2006).

The prevailing current direction, water velocities, and spatial extent of the ACC make it unlikely that advected fish return to the areas where they were spawned; although this could occur via a circum-Antarctic pathway, mesoscale gyre circulations, or by directed migration, our results suggest that in practise, their contribution is small, at least to structuring toothfish populations. On the other hand, advection would account for the nucleus chemistry distributions we found downstream of South Georgia. The SAF and PF transport water across the South Atlantic and into the Indian Ocean where, although the average position of the SAF lies north of the Kerguelen Plateau, the PF crosses immediately north of Kerguelen Island. As a result, life stages entrained in the PF at South Georgia could be advected directly to Kerguelen. Since the SAF frequently occupies a position over the Kerguelen Plateau, life stages so entrained could be advected to Macquarie Island and on to the southern Pacific. The staggered distribution found in toothfish suggested advection of this nature along the ACC; fish with early life histories similar to north and east South Georgia occurred in smaller proportions further downstream, while a new population at Kerguelen also occurred downstream at Macquarie, and another appeared first at Macquarie and then south of South Georgia.

### Complex population structure and management

If life stages of marine fish are advected by fronts, then physical processes governing frontal position may drive the rate of entrainment and abundance at downstream fishing areas. The proportions of fish mixing may be linked to frontal stability; for instance, if the proximity of the SAF to Kerguelen drives the supply of fish to Macquarie Island, their abundance at Macquarie may vary quite predictably, but lead to considerable temporal variability in mixing proportions as well as stock size.

Such linkages can undermine management if it is not coordinated between fishing areas; reducing the size of independent fishing areas is often held to be conservative (e.g., Smith and McVeagh 2000), but the size of the management area on its own is likely to have limited benefit if important sources of recruitment lie outside. Genetic heterogeneity between areas, however, as in the case of toothfish, implies that arriving fish do not breed with resident ones. Instead, advection may promote population structure consisting of members mixed with vagrants transported from spawning grounds upstream. Life history strategies to compensate for extensive losses of vagrants would explain the anomaly that some species have high fecundity rates like toothfish (e.g., Kock et al. 1985), an attribute associated with high mortality, yet are long-lived and grow slowly, features more often associated with low natural mortality (e.g., Jones and Wells 1998; Wells and Jones 2002). Moreover, restriction of the breeding population to a relatively small proportion of fish able to access spawning grounds would help account for cases where strong differentiation in mtDNA is not reflected in nuclear DNA (e.g., Appleyard et al. 2002; Shaw et al. 2004).

Even though they do not contribute reproductively, vagrants are important to fishermen. They may also mitigate fishing on adults that do spawn and form an important component of local ecosystems. As a result, interruption in the movement of fish, through fishing pressure upstream or changes in advection patterns driven by global warming (e.g., Hofmann and Murphy 2004), would have serious implications for productivity and conservation. By corollary, fishing effort directed on areas where breeding members concentrate may have disproportionate effects on abundance and genetic composition, locally and in fisheries downstream.

Identifying population structure correctly is therefore critical for sustaining fisheries. Although only genetic approaches can directly address gene flow, our results show that otolith chemistry can greatly illuminate the physical and population processes underlying genetic distributions and resolve complex population structures involving mixing. Resolution in turn can provide important insights with which to refine management strategy. In the case of Patagonian toothfish, catch taken off South America may depend on fish recruiting from other fishing areas. In the Antarctic, it may depend in part on advection rates along the ACC. However, between the two regions, the chemistry strongly supports exchange restricted by physical processes associated with the PF. By enabling new ways to detect mixing and separate populations, otolith chemistry can help managers resolve complex population structure driven by advection in oceanic systems.

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# Low genetic connectivity in an estuarine fish with pelagic larvae

**I.R. Bradbury, S.E. Campana, and P. Bentzen**

**Abstract:** We evaluated the spatial scale of metapopulation structure and genetic connectivity in rainbow smelt, *Osmerus mordax*, using eight microsatellite loci at 22 spawning locations throughout Newfoundland and Labrador. Consistent with low gene flow and limited dispersal, significant genetic structuring ($F_{ST}$ = 0.11) was present at small spatial scales (<200 km). Moreover, strong isolation by distance (IBD, $P < 0.001$, $r^2 = 0.47$) was observed, which was linear at small scales and nonlinear at large distances (>200 km). We hypothesized that despite high dispersal potential associated with a pelagic larval stage, behaviours restricting gene flow may result in structuring at the estuary scale. Multidimensional scaling and neighbour-joining of multilocus genotypes indicate some bay-scale associations. However, a comparison of $F_{ST}$ values and IBD residuals at both estuary and bay scales indicated low structure within and elevated structure among estuaries. Estuarine structuring was further supported by the presence of significant small-scale IBD within several coastal embayments (50–100 km), as well as Bayesian clustering consistent with estuarine-scale independence. Finally, estimates of dispersal based on the IBD relationship are consistent with local estuarine recruitment (<1.5 km·generation$^{-1}$). We conclude that the unexpectedly high genetic structure observed is consistent with behavioral influences reducing dispersal, supporting previous work implicating active larval retention.

**Résumé :** Nous avons déterminé l'échelle spatiale de la structure de la métapopulation et de la connectivité génétique chez l'éperlan arc-en-ciel, *Osmerus mordax*, à l'étude de huit locus microsatellites à 22 sites de fraie répartis sur l'ensemble de Terre-Neuve-et-Labrador. En accord avec le faible flux génique et la dispersion limitée, il y a une structuration génétique importante ($F_{ST}$ = 0,11) à de petites échelles spatiales (<200 km). De plus, nous observons une fort isolement par distance (IBD, $P < 0,001$, $r^2 = 0,47$) qui est linéaire à de petites échelles et non linéaire sur de grandes distances (>200 km). Nous posons en hypothèse que, malgré le potentiel élevé de dispersion associée au stade larvaire pélagique, des comportements qui restreignent le flux génique entraînent une structuration à l'échelle de l'estuaire. Un cadrage multidimensionnel et une analyse du plus proche voisin des génotypes à plusieurs locus indiquent l'existence de certaines associations à l'échelle de la baie. Cependant, une comparaison des valeurs de $F_{ST}$ et des résidus de l'IBD, tant à l'échelle de l'estuaire que de la baie, révèle une structure faible à l'intérieur des estuaires et une structure plus importante entre les estuaires. La structuration au niveau des estuaires est, de plus, établie par la présence d'une IDB significative à petite échelle à l'intérieur de plusieurs baies côtières (50–100 km), de même que par un regroupement bayésien compatible avec une indépendance à l'échelle de l'estuaire. Finalement, les estimations de la dispersion basées sur les relations des IBD sont compatibles avec un recrutement estuarien local (<1,5 km·génération$^{-1}$). Nous concluons que la structure génétique plus importante que prévue que nous observons est compatible avec l'existence d'influences comportementales qui réduisent la dispersion, ce qui est en accord avec des recherches antérieures qui concluent à une rétention active des larves.

[Traduit par la Rédaction]

## Introduction

Connectivity among demes in fragmented habitats is a key factor promoting the stability and persistence of metapopulations (e.g., Hanski 2001; Johst et al. 2002). Highly connected metapopulations may be guarded against extinction through the rescue effect (Brown and Kodrick-Brown 1977) or recolonization (Hanski 1999; Schtickzelle et al. 2006). The scale of connectivity is ultimately determined by habitat heterogeneity (i.e., structural connectivity) and dispersal patterns and mortality (i.e., functional connectivity). The degree of connectivity directly influences the scale of adaptive potential (Wright 1931), temporal persistence (Hanski 2001; Hastings and Botsford 2006), and ecosystem structure (e.g., Cowie and Holland 2006). Although measures of metapopulation dynamics and connectivity are com-

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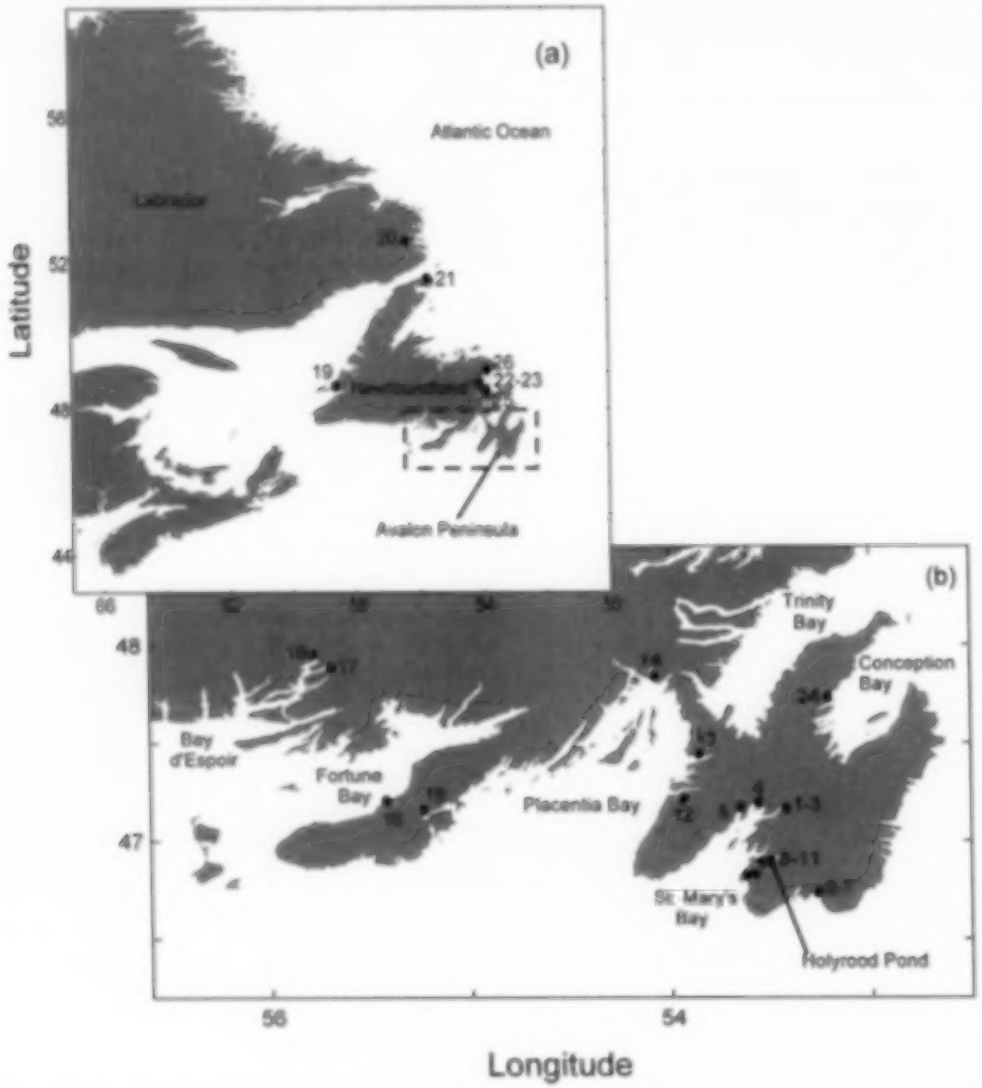
**Fig. 1.** (*a*) Map of study locations in Newfoundland and Labrador on the east coast of Canada. Inset (*a*) shows location of southeast coast of Newfoundland. Location numbers refer to locations in Table 1.




mon for terrestrial organisms such as insects (Hanski 1999), birds (Opdam 1991) or amphibians (Stevens et al. 2006), similar studies are comparatively rare for many marine environments (see Laurel and Bradbury 2006).

In marine species, the bipartite life history and pelagic larvae stage confer high dispersal potential (Palumbi 2003). Despite high dispersal potential and long-standing assumptions regarding the ubiquity of long-distance dispersal during the larval stage (e.g., Scheltema 1971), examples of marine species with strong genetic structure and low connectivity are increasingly common (e.g., Taylor and Hellberg 2003; Jones et al. 2005; Ruzzante et al. 2006). Alternate hypotheses regarding the prevalence of broad-scale gene flow are that resultant gene flow may be constrained or modified by behavioral contributions (e.g., Bradbury et al. 2003) or mortality (Cowen et al. 2000). Subsequently, predictions based on passive larval durations may substantially overestimate dispersal. Accordingly, high interspecific differences in the scale of marine connectivity and dispersal may be expected, despite the widespread presence of a pelagic larval stage (Hellberg et al. 2002).

Rainbow smelt (*Osmerus mordax*) is a small pelagic fish that is widely distributed in coastal and freshwater systems in northeastern North America (Nellbring 1989). Anadromous smelt spawn near the head of the tide in coastal rivers and streams, and the larvae develop in downstream estuaries (Ouellet and Dodson 1985; Bradbury et al. 2004). Prior work suggests important behavioural contributions to early life-history pattern in the form of synchronized hatch (Bradbury et al. 2004) and estuarine larval retention through diel vertical migration (Laprise and Dodson 1989; Bradbury et al. 2006*a*). The close association of smelt with estuarine

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**Table 1.** Locations, details, and summary genetic statistics for rainbow smelt (*Osmerus mordax*) samples from coastal Newfoundland and Labrador 2002–2006.

| Population (year) | Location | Sample size | $H_e$ | $H_o$ | Mean no. of alleles |
|---|---|---|---|---|---|
| 1. Salmonier River (2002) | St. Mary's Bay | 80 | 0.76 | 0.76 | 11.00 |
| 2. Salmonier River (2003) | St. Mary's Bay | 94 | 0.75 | 0.75 | 10.38 |
| 3. Salmonier River (2006) | St. Mary's Bay | 93 | 0.74 | 0.78 | 10.63 |
| 4. Colinet River (2003) | St. Mary's Bay | 94 | 0.74 | 0.76 | 11.63 |
| 5. North Harbour River (2004) | St. Mary's Bay | 94 | 0.74 | 0.77 | 10.88 |
| 6. Biscay Bay River (2003) | St. Mary's Bay | 94 | 0.72 | 0.71 | 9.88 |
| 7. Biscay Bay River (2006) | St. Mary's Bay | 93 | 0.70 | 0.67 | 9.00 |
| 8. Holyrood Pond Brook (2005) | Holyrood Pond (SMB) | 94 | 0.77 | 0.68 | 10.63 |
| 9. Holyrood Pond Park (2004) | Holyrood Pond (SMB) | 94 | 0.75 | 0.74 | 10.13 |
| 10. Deer Pond Brook (2004) | Holyrood Pond (SMB) | 41 | 0.72 | 0.73 | 8.88 |
| 11. Pathend Brook (2005) | Holyrood Pond (SMB) | 94 | 0.75 | 0.74 | 10.25 |
| 12. Southeast Placentia (2005) | Placentia Bay | 94 | 0.72 | 0.71 | 10.00 |
| 13. Long Harbour Brook (2004) | Placentia Bay | 79 | 0.71 | 0.73 | 7.75 |
| 14. North Harbour River (2003) | Placentia Bay | 80 | 0.70 | 0.66 | 8.75 |
| 15. Salt Pond Brook (2003) | Placentia Bay | 92 | 0.78 | 0.73 | 10.25 |
| 16. Garnish River (2004) | Fortune Bay | 74 | 0.81 | 0.77 | 11.38 |
| 17. Conne River (2004) | Bay d'Espoir | 94 | 0.75 | 0.72 | 11.13 |
| 18. Little River (2004) | Bay d'Espoir | 94 | 0.73 | 0.75 | 10.13 |
| 19. Smelt Brook, Point Amal (2004) | Port aux Port Penninsula | 80 | 0.84 | 0.83 | 14.25 |
| 20. Mary's Harbour (2004) | Labrador | 55 | 0.69 | 0.68 | 8.63 |
| 21. Pistolet Bay | Northern Peninsula | 76 | 0.80 | 0.73 | 9.63 |
| 22. Gambo River (2003) | Bonavista Bay | 80 | 0.77 | 0.66 | 11.38 |
| 23. Gambo River (2005) | Bonavista Bay | 80 | 0.78 | 0.64 | 11.00 |
| 24. Salmon Cove River (2005) | Conception Bay | 94 | 0.70 | 0.69 | 11.50 |
| 25. Chuff Brook (2006) | Bonavista Bay | 93 | 0.71 | 0.64 | 11.13 |
| 26. Traverse Pond (2006) | Bonavista Bay | 93 | 0.72 | 0.67 | 11.00 |

**Note:** For Holyrood Pond samples, SMB indicates St. Mary's Bay. $H_e$, expected heterozygosity; $H_o$, observed heterozygosity.

habitat and the potential for active (i.e., vertical migration) estuarine retention of larvae has lead several studies to conclude that population structure is likely linked to individual estuaries or retention areas (Bernatchez and Martin 1996). Nonetheless, studies to date have primarily used morphological (Frechet et al. 1983*a*), allozyme (Copeman 1977), or mtDNA (Taylor and Bentzen 1993) variation to examine smelt population structure. Moreover, population structure of smelt in mainland Canada is likely influenced by heavy exploitation or habitat degradation (e.g., McKenzie 1964). In contrast, the currently very limited commercial or recreational harvest within Newfoundland and Labrador offers a unique opportunity to study the species where anthropogenic influences have been minimal. Examination of genetic differentiation within the Pacific osmerid, eulachon (*Thaleichthys pacificus*), which possesses a similar life history, suggests divergence may be weak over large spatial scales (McLean and Taylor 2001; Beacham et al. 2005), contrary to hypotheses of estuarine isolation.

We utilize spatial variation at eight microsatellite loci to examine smelt population structuring and the degree of functional connectivity among spawning runs. We hypothesize that, in contrast with expectations for a species with an extensive pelagic larval period (~30 days at preflexion or the upward flexion of the notochord), populations are structured at the scale of individual estuaries in accordance with member–vagrant theory (e.g., Sinclair 1988; Bernatchez 1997). The overall goal here is to explore the potential consequences of behavioural retention in a species with an extensive pelagic larval period and mobile adults (Bradbury et al. 2006*a*) for the structuring of smelt metapopulations and the long-term evolutionary dynamics of the species.

## Materials and methods

### Study area

In total, 22 locations around Newfoundland and Labrador were sampled from 2003 to 2006 (Fig. 1, Table 1). Oceanographic and circulation conditions vary dramatically across the study; although the Labrador Current dominates coastal Newfoundland transport (Bradbury et al. 2000), there is considerable variation associated with different bays. The Cabot Strait, which is approximately 110 km across and 500 m deep, separates Newfoundland from the mainland to the south, and the Strait of Belle Isle (average width 18 km) separates Newfoundland from Labrador. Newfoundland's coastline is characterized by numerous large (>100 km in at least one axis) embayments (Fig. 1) for which limited data suggest potential retention times for pelagic eggs or larvae on the order of 20–40 days (e.g., deYoung and Sanderson 1995; Bradbury et al. 2000).

### Genetic analysis and differentiation statistics

Fish were collected with dip nets or fyke nets during the spawning period. Pectoral or caudal fin clips were taken and immediately placed in 95% ethanol. DNA was extracted fol-

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**Table 2.** Pairwise $F_{ST}$ above the diagonal and $p$ value below the diagonal for 26 samples of rainbow smelt (*Osmerus mordax*) from 22

| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 | — | 0.005 | 0.008 | 0.006 | 0.003 | 0.053 | 0.068 | 0.052 | 0.050 | 0.058 | 0.057 | 0.066 |
| 2 | 0.99 | — | 0.007 | 0.007 | 0.003 | 0.049 | 0.064 | 0.052 | 0.043 | 0.048 | 0.047 | 0.055 |
| 3 | 0.99 | * | — | 0.000 | 0.002 | 0.053 | 0.069 | 0.068 | 0.069 | 0.074 | 0.072 | 0.084 |
| 4 | 0.86 | * | 0.66 | — | 0.004 | 0.058 | 0.077 | 0.077 | 0.073 | 0.079 | 0.080 | 0.086 |
| 5 | 0.99 | 0.53 | 0.40 | 0.01 | — | 0.054 | 0.069 | 0.063 | 0.062 | 0.066 | 0.065 | 0.077 |
| 6 | * | * | * | * | * | — | 0.005 | 0.090 | 0.086 | 0.097 | 0.083 | 0.082 |
| 7 | * | * | * | * | * | 0.836 | — | 0.105 | 0.099 | 0.112 | 0.096 | 0.099 |
| 8 | * | * | * | * | * | * | * | — | 0.010 | 0.013 | 0.014 | 0.059 |
| 9 | * | * | * | * | * | * | * | 0.966 | — | 0.001 | 0.000 | 0.027 |
| 10 | * | * | * | * | * | * | * | * | 0.998 | — | 0.004 | 0.034 |
| 11 | * | * | * | * | * | * | * | * | 0.998 | 0.112 | — | 0.027 |
| 12 | * | * | * | * | * | * | * | * | * | * | * | — |
| 13 | * | * | * | * | * | * | * | * | * | * | * | * |
| 14 | * | * | * | * | * | * | * | * | * | * | * | * |
| 15 | * | * | * | * | * | * | * | * | * | * | * | * |
| 16 | * | * | * | * | * | * | * | * | * | * | * | * |
| 17 | * | * | * | * | * | * | * | * | * | * | * | * |
| 18 | * | * | * | * | * | * | * | * | * | * | * | * |
| 19 | * | * | * | * | * | * | * | * | * | * | * | * |
| 20 | * | * | * | * | * | * | * | * | * | * | * | * |
| 21 | * | * | * | * | * | * | * | * | * | * | * | * |
| 22 | * | * | * | * | * | * | * | * | * | * | * | * |
| 23 | * | * | * | * | * | * | * | * | * | * | * | * |
| 24 | * | * | * | * | * | * | * | * | * | * | * | * |
| 25 | * | * | * | * | * | * | * | * | * | * | * | * |
| 26 | * | * | * | * | * | * | * | * | * | * | * | * |

**Note:** An asterisk (*) indicates comparisons were significant at $p < 0.001$.

lowing the protocol of Elphinstone et al. (2003), modified to work with a 96-well filter plate and automated on a robotic liquid handling system (Perkin Elmer). Individuals were genotyped using polymerase chain reaction (PCR) conditions of 5 or 10 μL volumes containing 20–100 ng DNA, 1.5 mmol·L$^{-1}$ $MgCl_2$, 80 μmol·L$^{-1}$ each dNTP, 0.5 U (1 U ≈ 16.67 nkat) *Taq* DNA polymerase (New England Biolabs), 0.3 μmol·L$^{-1}$ for each primer (forward primers were end-labelled with HEX, or ROX dye), and 1× PCR buffer (10 mmol·L$^{-1}$ Tris–HCl, pH 8.3; 50 mmol·L$^{-1}$ KCl). Two temperature profiles were used for touchdown to allow for the possibility of multiplex PCRs. Touchdown PCR conditions were as follows: 94 °C for 2 min, followed by 4–5 cycles of 94 °C for 30 s, program-specific touchdown annealing temperatures ($T_a$) minus 1 °C per cycle for 30 s, 72 °C for 30 s, followed by 25–26 cycles where the $T_a$ was held constant at 4 °C below the starting temperature. A final extension was held at 72 °C for 5 min. Reactions were run on Eppendorf thermocyclers and imaged on an FMBioII system (Hitachi Genetic Systems). Eight microsatellite loci were used as follows: Omo1, Omo2, Omo3, Omo4, Omo5, Omo9, Omo15, and Omo16. See Coulson et al. (2006) for further details.

Genetic polymorphism was quantified by examination of the number of alleles and observed and expected heterozygosities using GENETIX (version 4.05.2, Belkhir et al. 2004). Tests for Hardy–Weinberg equilibrium (HWE) and linkage disequilibrium were done using FSTAT (version 2.9.3.3, Goudet 1995). $F$ statistics and significance were calculated using FSTAT and ARLEQUIN (Schneider et al. 2000). Relationships among locations were visualized using two approaches. First, pairwise $F_{ST}$ values were visualized in two-dimensional space using multidimensional scaling (MDS) conducted in Primer 5.2.2 (Clarke and Gorley 2001). Second, a neighbour-joining tree based on Cavalli Sforza and Edward chord distances and bootstrapped across loci (1000 replicates) was generated using Populations (Langella 1999) and visualized using TreeView version 1.6.6 (Page 1996).

## Spatial analysis

An analysis of molecular variance (AMOVA) partitioned observed genetic variance into components associated with geographic regions (i.e., bays) and was conducted using ARLEQUIN. The presence of isolation by distance (IBD) was assessed using least squares regression of linearized $F_{ST}$ against pairwise geographic distance. To assess the scale of linearity, regressions were done at increasing spatial scales and slope plotted against the maximum size of the spatial bin (e.g., Castric and Bernatchez 2003; Bradbury and Bentzen 2007). Geographic distance between each site was measured as the shortest distance following within 5 km of the coastline using charts and Google Earth 2004. All distances were measured three times and averaged.

Spatial autocorrelation measures were calculated independently using PASSAGE (Rosenberg 2001). Alleles present in less than 5% of samples were excluded because rare events may substantially bias autocorrelation metrics (Legendre and Legendre 1998). Two autocorrelation metrics were used: Moran's $I$ and Geary's $c$. Moran's $I$ (Moran 1950) is similar to Pearson's correlation coefficient in that it is based on product moment formulation and usually varies

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locations from coastal Newfoundland and Labrador (see Table 1 for sample locations and names).

| 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 | 21 | 22 | 23 | 24 | 25 | 26 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 0.145 | 0.071 | 0.104 | 0.090 | 0.144 | 0.134 | 0.055 | 0.098 | 0.072 | 0.120 | 0.112 | 0.138 | 0.171 | 0.146 |
| 0.141 | 0.061 | 0.116 | 0.092 | 0.149 | 0.142 | 0.064 | 0.103 | 0.066 | 0.118 | 0.112 | 0.136 | 0.170 | 0.142 |
| 0.162 | 0.083 | 0.120 | 0.098 | 0.147 | 0.148 | 0.072 | 0.110 | 0.081 | 0.134 | 0.127 | 0.147 | 0.179 | 0.161 |
| 0.159 | 0.085 | 0.12 | 0.100 | 0.151 | 0.149 | 0.074 | 0.113 | 0.083 | 0.139 | 0.131 | 0.149 | 0.185 | 0.168 |
| 0.156 | 0.081 | 0.120 | 0.099 | 0.152 | 0.148 | 0.069 | 0.111 | 0.078 | 0.130 | 0.123 | 0.142 | 0.176 | 0.156 |
| 0.145 | 0.075 | 0.112 | 0.103 | 0.133 | 0.122 | 0.080 | 0.108 | 0.095 | 0.128 | 0.120 | 0.134 | 0.186 | 0.163 |
| 0.163 | 0.090 | 0.113 | 0.108 | 0.142 | 0.132 | 0.097 | 0.115 | 0.109 | 0.143 | 0.136 | 0.145 | 0.201 | 0.181 |
| 0.128 | 0.080 | 0.099 | 0.085 | 0.134 | 0.122 | 0.046 | 0.114 | 0.062 | 0.079 | 0.068 | 0.122 | 0.140 | 0.088 |
| 0.122 | 0.048 | 0.092 | 0.080 | 0.134 | 0.126 | 0.049 | 0.118 | 0.046 | 0.084 | 0.077 | 0.121 | 0.151 | 0.099 |
| 0.146 | 0.059 | 0.106 | 0.084 | 0.148 | 0.136 | 0.061 | 0.125 | 0.057 | 0.096 | 0.087 | 0.138 | 0.165 | 0.108 |
| 0.128 | 0.046 | 0.103 | 0.087 | 0.141 | 0.139 | 0.050 | 0.126 | 0.046 | 0.084 | 0.078 | 0.124 | 0.150 | 0.099 |
| 0.137 | 0.023 | 0.124 | 0.095 | 0.145 | 0.140 | 0.070 | 0.143 | 0.056 | 0.112 | 0.105 | 0.138 | 0.172 | 0.128 |
| — | 0.139 | 0.126 | 0.115 | 0.131 | 0.152 | 0.085 | 0.179 | 0.115 | 0.127 | 0.124 | 0.092 | 0.187 | 0.159 |
| * | — | 0.117 | 0.104 | 0.150 | 0.146 | 0.081 | 0.156 | 0.069 | 0.138 | 0.130 | 0.142 | 0.2 | 0.157 |
| * | * | — | 0.070 | 0.095 | 0.107 | 0.083 | 0.137 | 0.075 | 0.118 | 0.120 | 0.135 | 0.179 | 0.161 |
| * | * | * | — | 0.073 | 0.087 | 0.076 | 0.090 | 0.057 | 0.101 | 0.096 | 0.116 | 0.150 | 0.140 |
| * | * | * | * | — | 0.032 | 0.108 | 0.137 | 0.103 | 0.118 | 0.118 | 0.109 | 0.171 | 0.156 |
| * | * | * | * | * | — | 0.113 | 0.122 | 0.122 | 0.117 | 0.109 | 0.112 | 0.181 | 0.153 |
| * | * | * | * | * | * | — | 0.122 | 0.046 | 0.047 | 0.041 | 0.088 | 0.102 | 0.071 |
| * | * | * | * | * | * | * | — | 0.139 | 0.127 | 0.129 | 0.167 | 0.214 | 0.178 |
| * | * | * | * | * | * | * | * | — | 0.074 | 0.068 | 0.107 | 0.127 | 0.101 |
| * | * | * | * | * | * | * | * | * | — | 0.001 | 0.076 | 0.078 | 0.049 |
| * | * | * | * | * | * | * | * | * | 0.99 | — | 0.078 | 0.062 | 0.040 |
| * | * | * | * | * | * | * | * | * | * | * | — | 0.144 | 0.113 |
| * | * | * | * | * | * | * | * | * | * | * | * | — | 0.051 |
| * | * | * | * | * | * | * | * | * | * | * | * | * | — |

between 1 (positive) and –1 (negative) autocorrelation values (Legendre and Legendre 1998). Geary's $c$ is usually inversely related to Moran's $I$, though differences have been described (Legendre and Legendre 1998). Geary's $c$ values of 0–1 indicate positive correlation, >1 indicates negative correlation, and $c = 1$ indicates no correlation.

### Bayesian clustering

Bayesian clustering was done using STRUCTURE version 2.0 (Pritchard et al. 2000) and tested whether predictions of structuring at the scale of spawning run were consistent with multilocus genetic data. This approach uses assumptions of HWE and linkage equilibria among loci, introduces population structure, and uses a Markov chain Monte Carlo (MCMC) algorithm to estimate the number of populations ($K$). The algorithm was run three times for each $K$ to ensure convergence of values and with a burn-in of 50 000 replications, 200 000 replications after burn-in, and $K$ ranging from 1 to 22.

### Dispersal distance estimation

Dispersal distance was estimated using the approach outlined in Rousset (1997) and Bradbury and Bentzen (2007). The product of effective organism density and dispersal distance ($d$) may be estimated using the slope ($b$) of the regression of $F_{ST}/(1 - F_{ST})$ against geographic distance. Specifically, $1/b = 4D\sigma^2$, where $D$ is the effective adult density (individuals·km$^{-1}$), and $\sigma^2$ is the variance of parent–offspring axial distance. Assuming symmetrical exponential dispersal, the IBD slope approximated by $4D\sigma^2$ was converted to $d$ using $d = 1/\sqrt{(2/\sigma^2)}$ (Buonaccorsi et al. 2004). This estimate was compared with the relationship from Kinlan and Gaines (2003), based on the equation $d = 0.0016(\text{IBD slope})^{-1.0001}$. The IBD slope was taken as the maximum slope from the iterative regression analysis to account for nonequilibrium conditions. Previous work suggests census estimates of smelt density in these habitats are approximately 5040 individuals·km$^{-1}$ (I.R. Bradbury, unpublished data). However, in the absence of effective population estimates, and because effective population size and census size usually differ by two–three orders of magnitude in marine and estuarine fish (Hansen et al. 2002; Arden and Kapuscinski 2003), a value of 50.40 individuals·km$^{-1}$ was also used and likely more representative of actual effective densities. In all cases, estimate variance was calculated as the standard deviation using the distribution and standard deviation of possible slope values and subsequently converted to dispersal distance using both approaches presented above.

## Results

### Genetic differentiation

Summary statistics for genetic samples are included in Table 1. An average of 86 (range = 41–94) fish were genotyped per location. The eight microsatellite loci revealed substantial genetic variation, with an average expected heterozygosity within populations of 0.74 (range = 0.64–0.83), and an average of 10.43 alleles within populations

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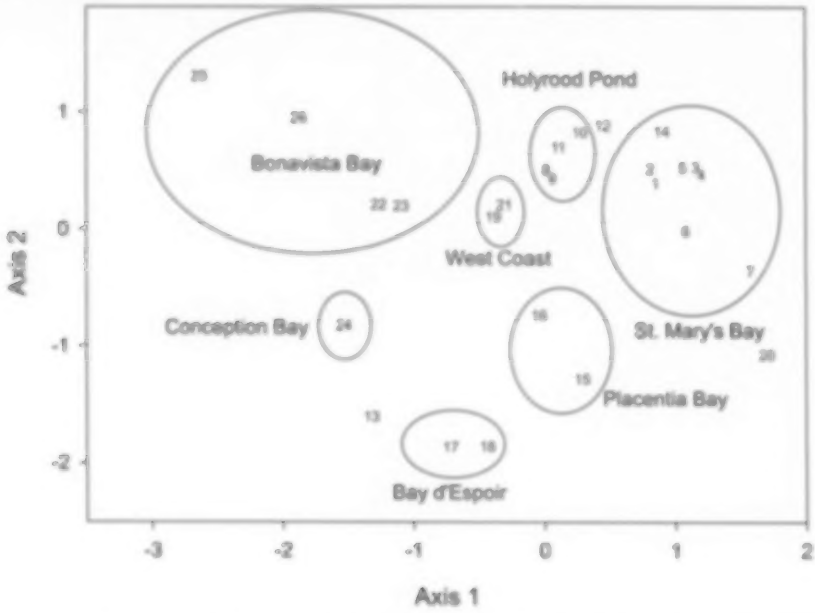
**Fig. 2.** Multidimensional scaling of multilocus genetic data for 22 spawning locations of anadromous rainbow smelt (*Osmerus mordax*) from Newfoundland and Labrador. Refer to Table 1 and Fig. 1 for sample and site details.



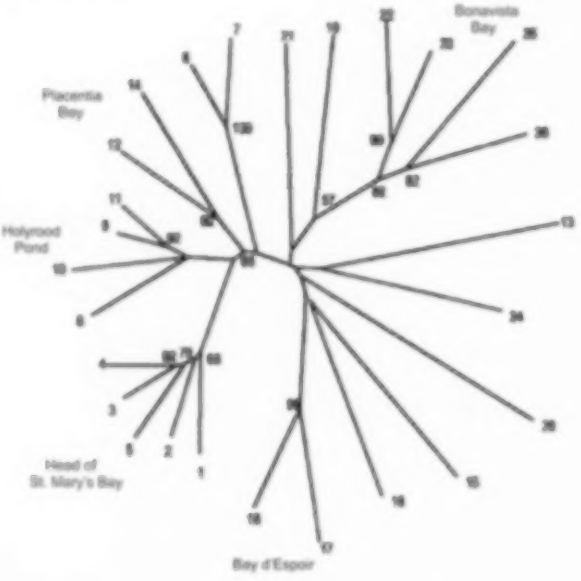

(range = 8–14). No evidence of linkage was observed. Deviations from HWE were observed at six locations and were primarily associated with Omo3 and Omo16. Tests for the presence of null alleles and scoring errors using MICRO-CHECKER (van Oosterhout et al. 2004) suggest that the presence of null alleles is rare (<5%) and primarily associated with Omo3 and Omo16. Because removal of either locus had no major effect on observed trends, they were included in further analyses. The estimate of global $F_{ST}$ was 0.11, which is indicative of significant structuring. Pairwise estimates of $F_{ST}$ (Table 2) among locations ranged from 0.002 to 0.23, and the majority of values were significant (>95%) with the exception of temporal replicates or locations from within a single estuary (e.g., Holyrood Pond). In all three locations with temporally replicated samples, comparisons were not significant among years (Table 2).

## Spatial analysis

MDS (Fig. 2) suggested the tendency for some spatial association (Kruskal stress = 0.15, $r^2$ = 0.87), although strict bay-scale associations were weak and limited to St. Mary's Bay. Neighbour-joining analysis of chord distances (Fig. 3) revealed that >50% bootstrap support was generally associated with nodes linking locations at small spatial scales, such as a Holyrood Pond group and a head of St. Mary's Bay group. Overall, there was limited evidence of bay-scale structure (i.e., clustering of all locations within an embayment). AMOVA results based on groups and outlier locations identified in MDS analysis suggest significant structuring at all levels (Table 3), and among-group variance explained 5.8% of the total variance ($p < 0.001$).

Significant isolation by distance was present at multiple spatial scales and was assessed using spatial autocorrelation and least squares regression. Autocorrelation metrics indi-

**Fig. 3.** Neighbour-joining dendrogram based on Cavalli Sforza and Edwards chord distances. See Table 1 for location key. Numbers on each node represent percentages of bootstrap support for each node.




cated significant positive correlations at small spatial scales. Moran's $I$ ranged from 0.8 to 0.2 at small distances, with a global estimate of 0.6. Values became negative between 100 and 150 km (Fig. 4*a*). Similarly, Geary's $c$ suggested significant positive correlations at small scales and reached a value of 1 at ~150 km (Fig. 4*b*), indicative of no association.

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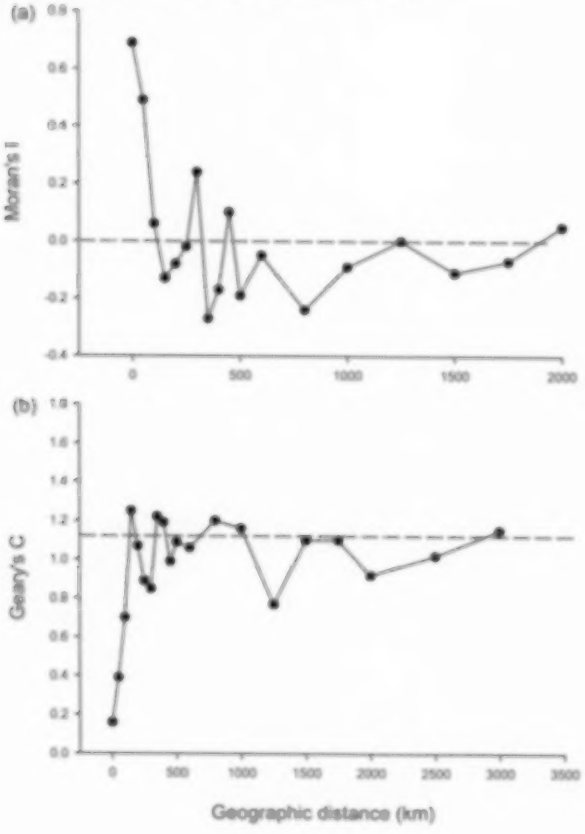
**Table 3.** Analysis of molecular variance (AMOVA) results comparing genetic variation among groups of rainbow smelt (*Osmerus mordax*) identified in multidimensional scaling analysis (Fig. 2) of populations sampled throughout Newfoundland and Labrador.

| Source of variation | df | Sum of squares | Variance component | Percentage of total | $F_{ST}$ | $F_{SC}$ | $F_{CT}$ |
|---|---|---|---|---|---|---|---|
| Among groups | 9 | 701.366 | 0.151 82 | 5.75 | 0.1073*** | | |
| Among populations within groups | 17 | 434.688 | 0.131 53 | 4.98 | | 0.05283*** | |
| Within populations | 4460 | 10 518.41 | 2.358 39 | 89.27 | | | 0.05747*** |
| Total | 4485 | 11 654.47 | 2.641 74 | 100 | | | |

**Note:** Asterisks (***) indicate significance at $\alpha = 0.05$.

**Fig. 4.** Moran's $I$ (*a*) and Geary's $c$ (*b*) correlograms for 22 locations of anadromous rainbow smelt from coastal Newfoundland and Labrador based on eight microsatellite loci.




Overall, regression between genetic differentiation and geographic distance indicated a nonlinear association ($r^2$ = 0.35, Fig. 5*a*). Isolation-by-distance linearity, measured as the $r^2$ of the linear regression, increased with scale of analysis until approximately 200 km, and the IBD slope decreased with increasing spatial scale, as would be expected, with a nonlinear trend at larger distances (Fig. 5*b*). To evaluate the scale of isolation, IBD was examined individually within three of the embayments (Fig. 6). In two of the comparisons (St. Mary's and Bonavista bays) significant IBD was present within each bay, and in the third comparison (Placentia Bay), elevated differentiation was present overall, although there was no increase with distance (Fig. 6). To examine the role of estuarine and bay structure in regulating gene flow, genetic differentiation was compared at both the bay and estuary scale (Fig. 7). Comparison of $F_{ST}$ values and residuals from the IBD plot suggested little structure among sites that share an estuary (i.e., low $F_{ST}$ and negative IBD residuals) but large structural differences between sites within an embayment (i.e., high $F_{ST}$ and higher residuals).

### Bayesian clustering

STRUCTURE analysis indicated a high number of populations based on Bayesian clustering. The values of –log Pr($X$/$K$), representing the estimated posterior probabilities of $K$, reached a plateau at 14 before becoming unstable (Fig. 8) and was consistent over multiple runs ($n$ = 3, Fig. 8).

### Dispersal distance estimation

Using an effective density estimate of 5040 individuals·km$^{-1}$, the dispersal estimate was 0.15 km·generation$^{-1}$, which increased using a more realistic and lower effective density of 50.40 individuals·km$^{-1}$, to an estimate of 1.4 ± 2.94 km·generation$^{-1}$. Using the relationship from Kinlan and Gaines (2003), we obtained an estimate of 1.33 ± 5.37 km·generation$^{-1}$.

## Discussion

The stability and resilience of marine species is likely linked to the connectivity of marine metapopulations (e.g., Hanski 1999; Johst et al. 2002; Kritzer and Sale 2006). Marine populations may be connected by the exchange of individuals either through pelagic larval transport or adult movement. Despite the ubiquity of a pelagic larval stage and inferred high dispersal potential, active retention or natal philopatry may have dramatic consequences for the connectivity and long-term evolutionary dynamics of marine ecosystems. We demonstrate significant small-scale genetic structuring and limited realized dispersal in rainbow smelt in coastal Newfoundland and Labrador, despite an extensive pelagic larval stage (i.e., approximately 30 days from hatch until flexion) and mobile adults. The results support the hypothesis that smelt populations are structured at the scale of the local estuary, which is consistent with the member–vagrant hypothesis and with a behavioural role in regulation of connectivity.

The linkage of smelt population structure to retention areas has been hypothesized by previous authors (e.g., Frechet et al. 1983*a*; Baby et al. 1991; Bernatchez and Martin 1996).

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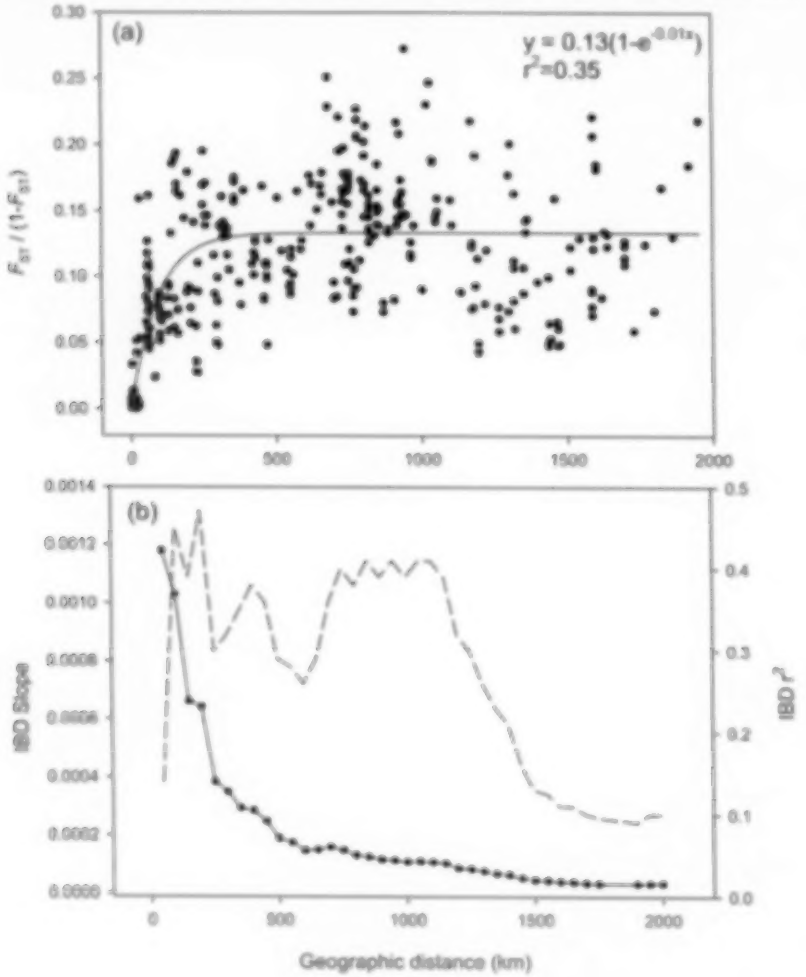
**Fig. 5.** (*a*) Isolation by distance (IBD) plot of linearized genetic divergence ($F_{ST}$) with geographic distance. Solid line represents nonlinear regression. (*b*) IBD slope (solid line) and $r^2$ (broken line) from iterative linear regression analysis at increasing bin sizes.




Spatial associations with morphology (Frechet et al. 1983*a*), parasites (Frechet et al. 1983*b*), and mtDNA (Bernatchez and Martin 1996) all support linkages to estuarine structure. Bradbury et al. (2006*b*) observed strong phenotypic differences among 10 locations along the south coast of Newfoundland and support the evolutionary independence of local estuaries. This present work supports these earlier findings and resolves the spatial scale of structuring and the delineation of predominant forces. In addition to the observed fine-scale genetic correlation, an absence of drift dispersal equilibrium was observed at large scales as indicated by the nonlinearity of the IBD relationship. This observation suggests a threshold of ~200 km, below which dispersal may influence spatial structure but beyond which genetic drift may dominate (Slatkin 1993).

The various clustering approaches suggest considerable fine-scale structuring, with only weak evidence of large-scale structure. Nodes suggested by clustering indicate all of the strongly supported branches are terminal and consistent with small-scale (e.g., estuarine) comparisons. The lack of support for the major branches supports the hypothesis of structuring at the scale of individual estuaries. The STRUCTURE analysis suggested the presence of ~14 significant clusters or populations. This number of clusters is inconsistent with structuring at the scale of spawning location. Given the presence of nonsignificant $F_{ST}$ values among sample sites sharing estuaries (e.g., Holyrood Pond and St. Mary's Bay), such an estimate may support structuring at the estuary scale, though even combining nearby locations that may share an estuary results in 16 clusters and not the observed 14. Nonetheless, this hypothesis of estuarine structure is further supported by the observation of significant isolation by distance within local embayments at scales of <100 km in both St. Mary's Bay and Bonavista Bay. Within Placentia Bay, this pattern was not observed; nonetheless, differentiation within Placentia Bay was substantial ($F_{ST}$ = 0.13). Similar trends were observed with the MDS analysis, where Placentia Bay lacked the genetic cohesion observed in some

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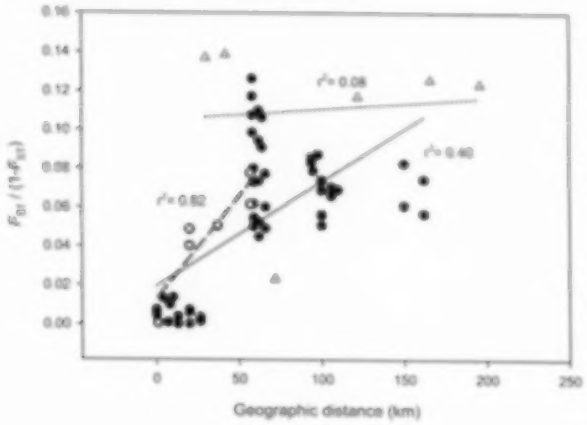
**Fig. 6.** Isolation by distance (IBD) relationships for three bays included in study analyzed separately. Solid circles represent St. Mary's Bay, open circles represent Bonavista Bay, and triangles represent Placentia Bay. Lines (solid, St. Mary's Bay; dashed, Bonavista Bay; dotted, Placentia Bay) represent least squares regression for each comparison.




of the other bays. These results may be linked to the fact that Placentia Bay is the largest bay and the samples were spaced further apart, making it difficult to resolve fine-scale differences.

Our estimates of dispersal distance coincide with dispersal restricted to single estuaries. The use of IBD relationships in the estimation of marine dispersal is gaining widespread use, yet it is subject to several assumptions and limitations (for a review see Bradbury and Bentzen 2007). Our estimates of dispersal using the approaches of Kinlan and Gaines (2003) and Rousset (1997) appear similar, with both approaches suggesting dispersal estimates of <1.5 km·generation$^{-1}$. Such estimates of dispersal are in direct agreement with estimates of larval transport in these habitats (Bradbury et al. 2006*a*) and with estimates of adult straying (McKenzie 1964).

As such, it seems behavioral modifications to dispersal and metapopulation connectivity likely result from either active larval retention or natal philopatry. Vertical migration in areas of strong shear has been implicated as a mechanism for larval smelt retention (Ouellet and Dodson 1985; Laprise and Dodson 1989). Bradbury et al. (2006*a*) examined larval transport within Salmonier estuary and suggested ontogenetic shifts in behavior may interact with seasonal hydrography to restrict larval transport to a single estuary. In contrast, adult tagging studies to date have primarily addressed spawning site fidelity and not natal philopatry. McKenzie (1964) documented annual homing rates of 90% to three streams within the Miramichi River. Nonetheless, estimates of annual site fidelity may differ dramatically from spawning natal fidelity, particularly if larval export is substantial. The role that natal homing may play in regulating smelt population structure is unclear. The genetic similarity observed here among locations within a single retention area or estuary (e.g., Holyrood Pond) suggests that if homing occurs within estuaries, its contribution may be secondary to that of the retention area. This is supported by a related study utilizing otolith elemental composition, which indi-

**Fig. 7.** Average (+ variance) $F_{ST}$ (*a*) and isolation by distance (IBD) residuals (*b*) for pairwise comparisons between sample locations sharing estuaries and bays. Data is based on linear portion of IBD (0–200 km).

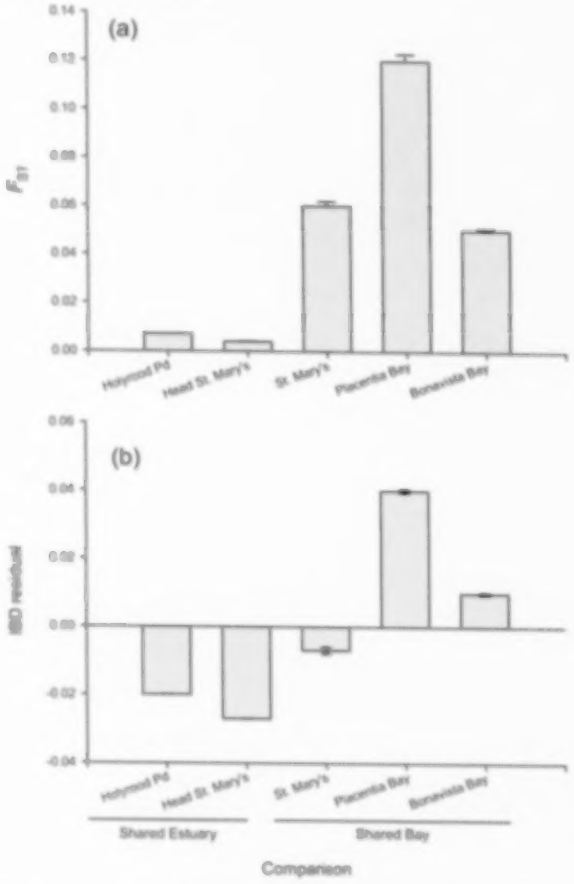
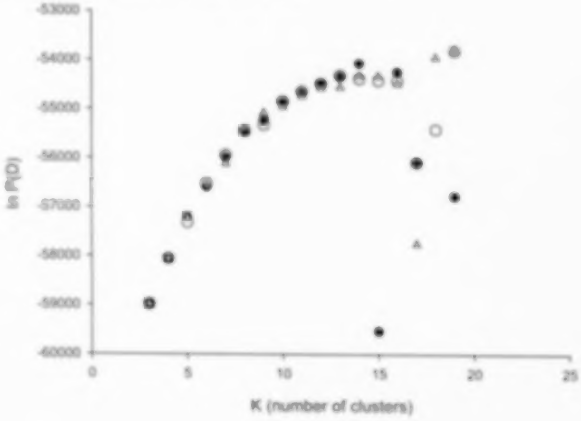



**Fig. 8.** Results from STRUCTURE analysis, ln *P*(*D*) with various values of *K* (1–22) for three replicates with 50 000 iterations burn-in and 200 000 after burn-in.

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cated that high rates of multiyear spawning site fidelity of smelt in these habitats results from strong habitat associations and not annual homing, as elemental composition suggests smelt rarely leave local estuaries (I.R. Bradbury, unpublished data).

Within other species of the family Osmeridae, the level of geographic differentiation typically seems low. McLean and Taylor (2001) and McLean et al. (1999) document spatial genetic structure over large distances (>2000 km) in a Pacific osmerid (*Thaleichthys pacificus*) with an anadromous life history and observed $F_{ST}$ values of 0.045 and 0.023 for microsatellite loci and mitochondrial sequence variation, respectively. Similarly, Beacham et al. (2005) used microsatellite loci in the same species and observed weak structure as well ($F_{ST} < 0.01$). Low estimates of divergence were also observed in capelin (*Mallotus villosus*) in the North Atlantic (Røed et al. 2003) with comparisons between the east and west Atlantic showing $F_{ST} = 0.03$ and a lack of significant differentiation within each region. Interestingly, even for rainbow smelt, the level of gene flow observed within Newfoundland and Labrador waters may be anomalously low (Bradbury et al. 2006*b*), and smelt from the mainland display genetic structuring indicative of marine species and other osmerids. These comparisons with other osmerids and rainbow smelt from elsewhere support a hypothesis of unusually high divergence and low connectivity for Newfoundland smelt. As such, it seems regional variation in gene flow and connectivity within a species or life history may be large, making generalizations difficult.

Admittedly, estimates of differentiation here are on par with other anadromous fish species (e.g., Hendry et al. 2004; Bradbury and Bentzen 2007). Comparisons of Atlantic salmon (*Salmo salar*) along the coast of Newfoundland encompassing many of the same sites indicate levels of divergence equal to our observations here (Palstra and Ruzzante 2007). However, as smelt lack the typical salmonid life history and are characterized by short upstream migrations and small pelagic marine larvae that exit the river within hours of hatching, this level of differentiation is unexpected. Examples of elevated genetic isolation and low connectivity have been noted in several marine and estuarine invertebrate (e.g., Lessios 1998; Perrin et al. 2004) and fish species (Adams et al. 2006). Nonetheless, the degree of structure observed here remains unexpectedly high ($F_{ST} \approx 0.12$). Reports of differentiation in other estuarine fishes suggest moderate ($F_{ST} \sim 0.003$–$0.02$) levels of connectivity (Beheregaray and Sunnucks 2001; Adams et al. 2006); and in marine fishes, low ($F_{ST} < 0.01$) differentiation and relatively high connectivity appear the norm (Bentzen et al. 1996; Jorgensen et al. 2005). Levels of gene flow and differentiation observed within other osmerids (e.g., McLean and Taylor 2001; Beacham et al. 2005) are consistent with these examples of marine and estuarine species, again highlighting the elevation of differentiation among Newfoundland smelt samples. Whether the low connectivity of smelt populations in Newfoundland waters is a result of local adaptation in the form of larval behavior, adult homing abilities, or some other cause is unknown and ultimately requires further evaluation.

The interaction of genetic connectivity and spatial scale can allow inference of dominant evolutionary processes (Slatkin 1993). At dispersal drift equilibrium, a monotonic relationship between genetic differentiation and geographic distance should be present (Slatkin 1993). The scale at which equilibrium will be apparent will be dependent both on the dispersal kernel of the species and the time since colonization. The observation of significant isolation by distance over small to moderate geographic scales suggests that the 10 000 years since the last glacial retreat in eastern Canada has been sufficient for equilibrium to be established on scales of up to 200 km. Moreover, the observation of a maximum $F_{ST}$ at scales larger than 200 km suggests nonequilibrium conditions at larger scales, likely as a result of the combined effects of limited dispersal and recent colonization. Similar trends in a declining IBD slope with distance have been observed elsewhere (e.g., Castric and Bernatchez 2003; Bradbury and Bentzen 2007).

The consequences of low connectivity for the stability and persistence of metapopulations can be profound (Hanski 1999). Classical metapopulation models suggest that persistence is dependent on a balance between dispersal–colonization rate and extinction rate (Hanski 1999). Connectivity directly determines the contribution of recolonization of extinct, vacant habitats and buffering of stochastic environmental influences in occupied habitats. Without the stabilizing influences of gene flow, local populations may be extremely vulnerable to disturbance and extinction pressure. In light of the limited dispersal that connects these smelt spawning locations and given the ephemeral nature of smelt spawning habitat, it appears that smelt populations in Newfoundland and Labrador may be more susceptible to disturbance than other marine or anadromous species. Furthermore, it seems that connectivity and metapopulation dynamics beyond the scale of local embayments may be quite limited in smelt in Newfoundland, as dispersal at these scales appears uncommon and the likely scenario is one of a series of disconnected metapopulations within local embayments.

In conclusion, these results show significant genetic structuring and low connectivity in rainbow smelt over large and small spatial scales. The observed high genetic isolation appears at odds with pelagic larval dispersal. These results contribute to a growing body of evidence suggesting that large interspecific variation exists in spatial complexity and genetic structure within marine species, despite the dispersal potential of the pelagic larval stage. Strong heterogeneity in population spatial structure among marine and estuarine species suggests substantial differences in the processes and mechanisms that maintain metapopulations. We suggest that studies such as this, which identify the critical scale of connectivity within a marine species, will be essential to the understanding and management of marine ecosystems.

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# Temporal variation in fish egg and larval production by pelagic and bottom spawners in a large Newfoundland coastal embayment

**Paul V.R. Snelgrove, Ian R. Bradbury, Brad deYoung, and Sandra Fraser**

**Abstract:** In highly seasonal environments such as coastal Newfoundland, local production, advection, and life history may influence ichthyoplankton community structure. The spring bloom occurs in cold water that slows development of eggs from pelagic spawners and may transport propagules from optimal nearshore areas before hatch. For bottom spawners that affix eggs to the bottom, the problem is reduced because only actively swimming larval stages are pelagic. We hypothesize that larvae of pelagic spawners are limited to warmer, summer waters, whereas larvae of bottom spawners are less constrained temporally and less subject to flushing from the nearshore environment. Ichthyoplankton taxa sampled in Placentia Bay, Newfoundland, during spring–summer in 1997–1999 showed consistent seasonal peaks in egg and larval abundance. Although pelagic egg production spanned spring and summer, larval abundance peaked late in summer or early fall in the most productive areas of the bay. Larval abundance of bottom spawners peaked in spring for most taxa. Thus, pelagic eggs hatch quickly in summer, and larvae can utilize the late peak in nearshore copepod abundance. Bottom spawners can utilize spring zooplankton because temperature-dependent development does not influence egg advection. Coastal advection and temperature influence how different life history groups exploit spatial and temporal peaks in production.

**Résumé :** Dans les environnements fortement saisonniers, tels que la côte de Terre-Neuve, la production locale, l'advection et le cycle biologique peuvent influencer la structure de la communauté de l'ichtyoplancton. Le foisonnement des algues au printemps se produit en eau froide qui ralentit le développement des oeufs des reproducteurs pélagiques et peut éloigner les propagules des sites optimaux près des côtes avant l'éclosion. Chez les reproducteurs benthiques qui fixent leurs oeufs au fond, le problème est moins important seulement parce que les seuls stades à nage active sont pélagiques. Notre hypothèse veut que les larves des reproducteurs pélagiques soient restreintes aux eaux estivales plus chaudes et que les larves des reproducteurs benthiques soient moins limitées dans le temps et moins sujettes à être entraînées loin de l'environnement côtier. Les taxons de l'ichtyoplancton échantillonnés dans la baie de Placentia, Terre-Neuve, au printemps et à l'été 1997–1999 accusent des maximums cohérents d'abondance d'oeufs et de larves. Bien que la production pélagique des oeufs s'étende sur tout le printemps et l'été, l'abondance des larves atteint un sommet en fin de l'été ou au début de l'automne dans les régions les plus productives de la baie. L'abondance larvaire de la plupart des espèces à reproduction benthique est maximale au printemps. Ainsi, les oeufs pélagiques éclosent rapidement en été et les larves peuvent utiliser le pic tardif d'abondance des copépodes côtiers. Les reproducteurs benthiques peuvent profiter du zooplancton printanier, car le développement dépendant de la température n'affecte pas l'advection des oeufs. La température et l'advection sur la côte influencent comment les groupes à cycles biologiques différents exploitent les maximums spatiaux et temporels de production.

[Traduit par la Rédaction]

## Introduction

Early life history stages have long been thought to be critical for recruitment success (e.g., Hjort 1914; Horwood et al. 2000) and the establishment of spatial pattern of marine fish assemblages (e.g., Sherman et al. 1984; Hare et al. 1999). For most marine species, mortality during this period is extremely high, and there has been considerable discussion on the importance of matching larval hatching with availability of food (Hjort 1914; Cushing 1990), low predator abundance

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(Frank and Leggett 1982, 1983), and appropriate habitats (Frank and Leggett 1982; deYoung and Rose 1993). Recent emphasis has been placed on circulation patterns and their importance to local retention near suitable habitat (e.g., Jones et al. 1999; Swearer et al. 1999; Cowen et al. 2000). Availability of food and appropriate habitat are heavily dependent on how circulation patterns regulate distribution of eggs and early larval stages (e.g., deYoung and Rose 1993; Davidson and deYoung 1995; Bradbury et al. 2000), and in strongly seasonal environments, these relationships are further complicated by temperature-dependent development rates that may prolong hatching time and obfuscate any link between specific spawning location and hatching site (Bradbury et al. 2000). For species that produce pelagic eggs (hereafter pelagic spawners), the role of circulation and spawning location are even more pronounced than for species that spawn on the bottom and affix their eggs to the substrate so they do not disperse (hereafter bottom spawners). Hatched larvae have a relatively greater capacity than pelagic eggs to influence their own transport and spatial pattern, suggesting that passive dispersal in pelagic spawners is likely to be more pronounced than in bottom spawners. Work on reef fishes (e.g., Kingsford and Choat 1989; Hickford and Schiel 2003) suggests that there is no simple relationship between dispersal and developmental mode, but temporal persistence of patterns in larvae from bottom spawners relative to pelagic spawners led Suthers and Frank (1991) to suggest that pelagic spawner larvae may disperse further.

Coastal environments may be advantageous as a larval habitat for several reasons. Food may be more abundant than in shelf environments (Frank and Leggett 1982; Taggart and Leggett 1987; Bailey et al. 1995), predators may be less abundant (Frank and Leggett 1982), and critical habitat for bottom spawners and nursery habitat for juveniles may be more readily available (Ellertsen et al. 1981; Gotceitas et al. 1997). Coastal waters are often warmer than offshore areas, potentially resulting in reduced egg development times (Pepin 1991; Bradbury et al. 2000) and increased larval growth rates (Bailey et al. 1995). Faster growth may also reduce mortality resulting from predation on eggs and small, vulnerable larvae (Houde 1996). Thus, regardless of the taxonomic affiliation or adult habitat and ecological niche occupied by a given species, there may be considerable survival advantage in placing hatching larvae in a food-rich, coastal environment, particularly in temperature conditions that favour rapid egg development and (or) larval growth.

The goal of our study was to examine temporal variation in ichthyoplankton patterns in pelagic and bottom-spawning species through the spring and summer reproductive season in a large coastal embayment where physical variables exhibit strong variability in space and time. Placentia Bay is a large embayment on the south coast of Newfoundland that is characterized by strong cyclonic flow. Unlike the smaller embayments in the region for which ichthyoplankton has been studied (e.g., Frank and Leggett 1982; Laprise and Pepin 1995; Pepin et al. 1995), flow conditions are generally temporally consistent, at least along the sides of the bay, and are not as strongly coupled to changes in wind forcing (Bradbury et al. 2000; Schillinger et al. 2000). Moreover, the strength and consistency in predominant flow creates an additional problem for the retention of propagules within the coastal environment, in that spawning in some areas of the bay may lead to immediate and predictable flushing into the offshore environment.

We hypothesized that timing of larval peaks would coincide with peak food availability (Cushing 1990) and (or) periods when development times would be minimized, but that this pattern would depend on spawning strategy. For pelagic spawners, we predicted that spawning would occur in mid- to late summer, at locations and in temperature conditions where eggs would develop quickly in warm summer waters and larvae would hatch in the nearshore environment before being flushed from the bay. For bottom spawners, we predicted that protracted spawning would predominate because advective loss of their planktonic larvae, which have some swimming capacity, was expected to be less than that for pelagic eggs (e.g., Suthers and Frank 1991), particularly during the spring bloom. Egg development for bottom spawners could occur slowly in the bottom environment during late winter without advective loss from nearshore areas. Finally, we asked whether eggs of pelagic spawners are released "upstream" of areas of higher secondary production (e.g., Munk et al. 1995), thereby placing larvae in a favourable environment, and whether this pattern is similar to that observed in larvae of bottom spawners. These questions are addressed in the spatially and temporally dynamic context of Placentia Bay circulation and flushing, with the goal of understanding how spawning strategies link to coastal dynamics in seasonal environments.

## Materials and methods

The Placentia Bay study area is a large embayment (~130 km long by ~100 km wide at its southern mouth) on the southeast coast of Newfoundland (Fig. 1). Bottom depths are several hundred metres in the deepest channels that pass between scattered banks, and elongated islands divide the northern portion of the bay into three channels. Currents flow into the bay along the eastern side towards the north and in a southerly direction out of the bay along the western side; currents near the head of the bay and near the center of the bay are weaker and more variable (Bradbury et al. 2000; Schillinger et al. 2000).

Ichthyoplankton samples were collected on a grid of 45 stations along six parallel transects (see Fig. 1) that were 8 nautical miles (1 n.mi. = 1.853 km) apart and ran perpendicular to the long axis of the bay. Stations were 4 n.mi. apart along each transect, except where landmasses or bottom topography required that they be shifted slightly. The mouth of a Tucker trawl (2 m × 2 m) with decreasing mesh sizes of 1000, 570, and 333 μm was equipped with two General Oceanic flowmeters to allow estimates of flow volumes. Oblique tows at a towing speed of two knots (1 knot = 1.853 km·h$^{-1}$) were collected for 15 min to a maximum depth of 40 m. Previous studies in coastal Newfoundland have found that >95% of the ichthyoplankton occurs in the upper 40 m (Frank and Leggett 1982; Laprise and Pepin 1995). The Tucker trawl is a more effective sampler than bongo nets because it results in higher estimates of species diversity and lower variability, although the Tucker trawl may slightly underestimate larvae <5 mm (Pepin and Shears 1997). Cruises took place in April, June, and August of

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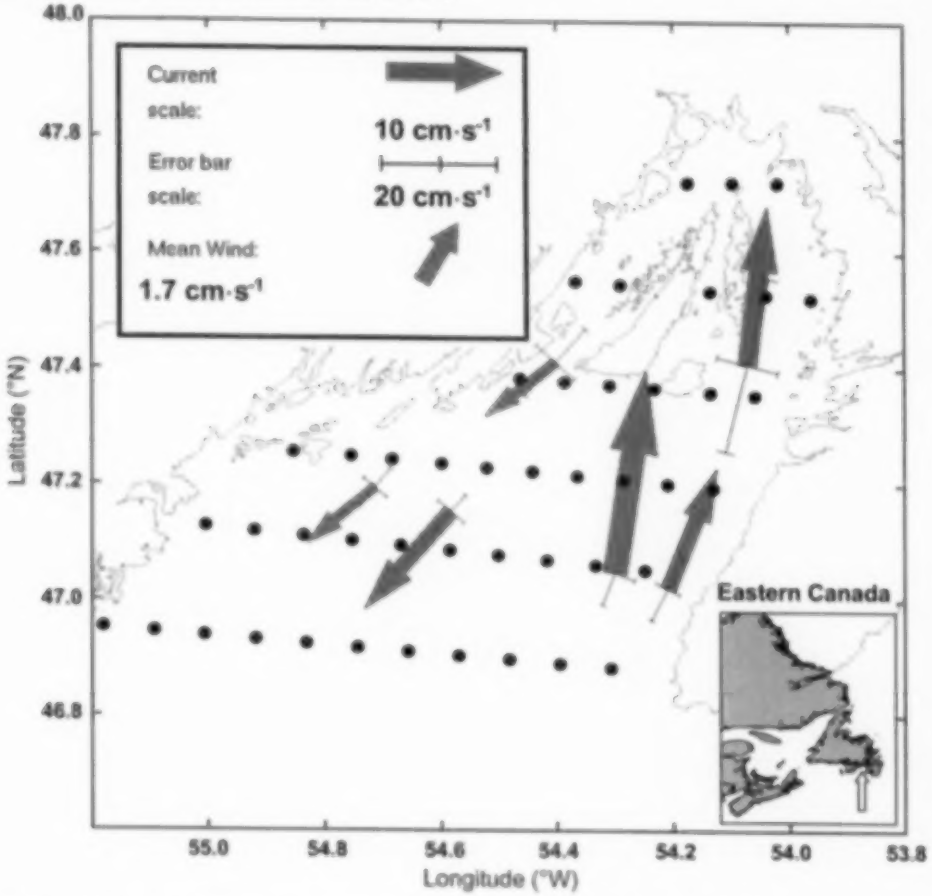
**Fig. 1.** Chart showing Placentia Bay ichthyoplankton sampling stations. Solid arrows denote mean circulation at a depth of 20 m for days 108–178, 1999. The results of covariance analysis are indicated in the figures by the solid axes. These axes show the standard deviation of the current along the direction of maximum variance and perpendicular to it. The scales for the current velocity and the variance are included in the left-hand corner. The mean wind velocity is included with the scales. Lower inset shows Atlantic Canada and Newfoundland; open arrow indicates location of Placentia Bay.




1997, 1998, and 1999; additional cruises took place in May 1997 and September 1998. Not all stations in the outer bay were sampled in the April and September trips because of weather and time constraints, and a few stations were missed during other cruises for similar reasons. These stations were therefore excluded for those time periods when they were not sampled.

Ichthyoplankton samples were preserved in 4% buffered formalin in seawater. In the laboratory, egg or larval taxa represented by >300 individuals were subsampled with a Motoda splitter (except April and June 1998, which were processed by the Atlantic Reference Center and subsampled as per Van Guelpen et al. 1982). All eggs and larvae were identified to the lowest taxonomic level possible. Eggs were grouped into four developmental stages using the scheme of Markle and Frost (1985). Although eggs of the *Gadus morhua* – *Melanogrammus aeglifinus* – *Glyptocephalus cynoglossus* (Atlantic cod – haddock – witch flounder) complex are difficult to differentiate during the first three developmental stages, we assumed from large differences in the relative abundances of larvae that the vast majority of eggs were Atlantic cod. A similar line of logic was used in assuming *Enchelyopus cimbrius* (fourbeard rockling) eggs were the major constituent of the *E. cimbrius* – hakes complex. The absence of hake larvae precluded resolution to species for this taxon. A similar assumption could not be made with the *Tautogalabrus adspersus* – *Limanda ferruginea* (cunner – yellowtail flounder) egg complex because larvae of both species were relatively common. Mean larval sizes (nearest 0.5 mm) were determined within each cruise for every taxon represented by more than five individuals within a given cruise.

Zooplankton in Tucker trawls were enumerated by subsampling with a Motoda splitter so that at least 300 individuals were counted per sample. The full sample was also examined to enumerate large taxa that were relatively low in abundance and therefore poorly estimated in subsamples. At each of the stations where ichthyoplankton–zooplankton samples were taken, vertical CTD (conductivity–temperature–depth sensor) casts were collected using either a Seabird 19

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**Table 1.** Average egg and larval concentrations (individuals·(1000 $m^3$)$^{-1}$) for pelagic spawners in Placentia Bay, 1997–1999.

| | | April | | | May | June | | | August | | | September |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Pelagic spawners | | 1997 | 1998 | 1999 | 1997 | 1997 | 1998 | 1999 | 1997 | 1998 | 1999 | 1998 |
| Gadidae | | | | | | | | | | | | |
| *Enchelyopus cimbrius* – hakes | Eggs | 0.00 | 0.00 | 0.00 | 0.00 | 0.05 | 4.42 | 5.47 | 1.47 | 1.01 | 1.84 | 2.77 |
| *Enchelyopus cimbrius* | Larvae | 0.04 | 0.00 | 0.00 | 0.00 | 0.00 | 0.06 | 0.00 | 2.62 | 1.12 | 0.50 | 1.71 |
| *Gadus morhua* – *Glyptocephalus cynoglossus* | Eggs | 663.59 | 122.60 | 119.33 | 171.83 | 194.19 | 181.75 | 181.97 | 23.01 | 86.15 | 81.36 | 20.30 |
| *Gadus morhua* | Larvae | 0.00 | 0.00 | 0.26 | 0.03 | 0.04 | 0.06 | 0.20 | 0.29 | 7.71 | 0.88 | 2.72 |
| *Pollachius virens* | Eggs | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.02 |
| | Larvae | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.02 | 0.00 | 0.00 | 0.00 | 0.00 | 0.06 |
| Labridae–Pleuronectidae | | | | | | | | | | | | |
| *Glyptocephalus cynoglossus* | Larvae | 0.00 | 0.00 | 0.02 | 0.00 | 0.00 | 0.00 | 0.47 | 0.45 | 0.53 | 0.48 | 0.39 |
| *Hippoglossoides platessoides* | Eggs | 25.17 | 10.57 | 57.81 | 82.05 | 8.83 | 77.95 | 130.51 | 2.27 | 5.00 | 2.14 | 0.70 |
| | Larvae | 0.00 | 0.00 | 0.01 | 0.00 | 0.00 | 0.32 | 0.53 | 0.08 | 0.62 | 0.16 | 0.11 |
| *Limanda ferruginea* | Larvae | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.44 | 0.10 | 0.26 | 0.16 | 0.01 |
| *Tautogalabrus adspersus* – *Limanda ferruginea* | Eggs | 0.01 | 0.00 | 0.00 | 0.00 | 18.53 | 23.35 | 77.95 | 1475.92 | 900.41 | 841.25 | 3.41 |
| *Tautogalabrus adspersus* | Larvae | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.01 | 0.00 | 609.01 | 359.87 | 407.21 | 58.84 |
| Scopthalmidae | | | | | | | | | | | | |
| *Scophthalmus aquosus* | Larvae | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.02 | 0.07 | 0.00 | 0.00 | 0.00 | 0.00 |
| Other eggs | | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.02 | 0.00 |
| Pelagic taxa | Eggs | 688.78 | 133.17 | 177.13 | 253.88 | 221.60 | 287.47 | 395.90 | 1502.68 | 992.57 | 926.59 | 27.19 |
| | Larvae | 0.04 | 0.00 | 0.29 | 0.03 | 0.04 | 0.49 | 1.72 | 612.54 | 370.11 | 409.39 | 63.84 |
| Total | | 688.82 | 133.17 | 177.43 | 253.91 | 221.68 | 287.96 | 397.62 | 2115.22 | 1362.69 | 1335.98 | 91.07 |



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**Table 2.** Larval concentrations (individuals·(1000 $m^3$)$^{-1}$) for bottom spawners in Placentia Bay, 1997–1999.

| | | April | | | May | June | | | August | | | September |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Bottom spawners | | 1997 | 1998 | 1999 | 1997 | 1997 | 1998 | 1999 | 1997 | 1998 | 1999 | 1998 |
| Agonidae | | | | | | | | | | | | |
| *Agonus decagonus* | Larvae | 0.00 | 0.00 | 0.02 | 0.00 | 0.00 | 0.03 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| *Aspidophoroides* sp. | Larvae | 0.25 | 0.00 | 0.20 | 0.08 | 0.03 | 0.06 | 0.03 | 0.02 | 0.00 | 0.00 | 0.00 |
| Ammodytidae | | | | | | | | | | | | |
| *Ammodytes* sp. | Larvae | 64.05 | 8.79 | 18.66 | 47.37 | 4.20 | 15.99 | 9.12 | 0.01 | 0.00 | 0.02 | 0.01 |
| Anarichadidae | | | | | | | | | | | | |
| *Anarhichas lupus* | Larvae | 0.07 | 0.13 | 0.11 | 0.00 | 0.00 | 0.01 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| Clupeidae | | | | | | | | | | | | |
| *Clupea harengus* | Larvae | 0.00 | 0.02 | 0.08 | 0.00 | 0.00 | 0.10 | 0.01 | 0.00 | 0.00 | 0.00 | 0.52 |
| Cottidae | | | | | | | | | | | | |
| *Gymnocanthus tricuspis* | Larvae | 0.00 | 0.28 | 0.02 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| *Icelus bicornis* | Larvae | 0.00 | 0.16 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| *Myoxocephalus aenaeus* | Larvae | 0.04 | 0.01 | 0.38 | 0.00 | 0.22 | 0.00 | 0.00 | 0.00 | 0.00 | 0.01 | 0.00 |
| *Myoxocephalus octodecemspinosus* | Larvae | 1.48 | 0.67 | 0.08 | 0.14 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| *Myoxocephalus scorpius* | Larvae | 2.72 | 1.41 | 1.53 | 0.26 | 0.03 | 0.01 | 0.06 | 0.00 | 0.00 | 0.00 | 0.00 |
| *Triglops* sp. | Larvae | 0.01 | 0.06 | 0.04 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| Cyclopteridae | | | | | | | | | | | | |
| *Cyclopterus lumpus* | Larvae | 0.02 | 0.00 | 0.00 | 0.02 | 0.00 | 0.01 | 0.01 | 0.00 | 0.07 | 0.06 | 0.02 |
| *Liparis* spp. | Larvae | 0.01 | 0.87 | 0.95 | 1.12 | 0.10 | 2.98 | 1.62 | 0.33 | 0.37 | 0.45 | 0.08 |
| Gadidae | | | | | | | | | | | | |
| *Gadus ogac* | Larvae | 0.02 | 0.14 | 0.90 | 0.00 | 0.00 | 0.00 | 0.02 | 0.00 | 0.00 | 0.00 | 0.00 |
| Hemitripteridae | | | | | | | | | | | | |
| *Hemitripterus americanus* | Larvae | 0.03 | 0.01 | 0.35 | 0.00 | 0.00 | 0.00 | 0.01 | 0.00 | 0.00 | 0.00 | 0.00 |
| Labridae–Pleuronectidae | | | | | | | | | | | | |
| *Pleuronectes americanus* | Larvae | 0.00 | 0.00 | 0.00 | 0.00 | 0.03 | 0.59 | 0.49 | 0.12 | 0.01 | 0.06 | 0.04 |
| Osmeridae | | | | | | | | | | | | |
| *Mallotus villosus* | Larvae | 0.11 | 0.50 | 0.01 | 0.00 | 0.02 | 0.00 | 0.01 | 700.23 | 467.54 | 101.72 | 486.09 |
| Pholidae | | | | | | | | | | | | |
| *Pholis gunnellus* | Larvae | 0.01 | 0.37 | 1.03 | 0.02 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| Scombridae | | | | | | | | | | | | |
| *Scomber scombrus* | Larvae | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.94 | 0.77 | 0.05 | 0.01 |
| Scorpaenidae | | | | | | | | | | | | |
| *Sebastes* sp. | Larvae | 0.18 | 0.01 | 0.00 | 0.00 | 0.03 | 0.12 | 0.11 | 3.91 | 1.12 | 1.98 | 0.45 |
| Stichaeidae | | | | | | | | | | | | |
| *Lumpenus* sp. | Larvae | 0.20 | 0.20 | 0.17 | 0.02 | 0.20 | 0.00 | 0.01 | 0.01 | 0.00 | 0.00 | 0.00 |
| *Stichaeus punctatus* | Larvae | 0.32 | 0.09 | 0.25 | 9.46 | 0.07 | 0.14 | 0.02 | 0.00 | 0.00 | 0.00 | 0.00 |
| *Ulvaria subbifurcata* | Larvae | 0.21 | 0.00 | 0.16 | 0.00 | 0.23 | 5.94 | 10.29 | 3.40 | 0.39 | 1.21 | 0.08 |
| Unidentified | Larvae | | | 0.00 | | | | 0.05 | | | 0.70 | |
| Bottom spawner totals | Larvae | 69.73 | 13.73 | 24.95 | 58.49 | 5.16 | 25.97 | 21.85 | 708.96 | 470.28 | 106.25 | 487.30 |
| Bottom spawner totals minus *Mallotus villosus* | Larvae | 69.62 | 13.23 | 24.94 | 58.49 | 5.14 | 25.97 | 21.85 | 8.73 | 2.74 | 4.53 | 1.21 |



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(May and June 1997) or Seabird 25 (all other cruises). These casts made it possible to contrast mixed-layer temperatures by averaging the upper 40 m from each profile.

### Data analysis

Ichthyoplankton abundances were divided by the volume filtered and expressed as the number of individuals·(1000 $m^3$)$^{-1}$. Temporal trends in total concentration of individuals were examined by plotting average concentrations for the total bay with standard errors. Bar charts provided a means of comparing egg stage composition over time, where each value represented the mean of all stations sampled in a given cruise. Temporal trends in dominant larval taxa were compared by plotting all observations versus the sampling date. These temporal scattergram plots permit an intuitive view of presence or absence as well as concentrations, which are confounded by very high spatial variability within a cruise.

To provide a summary representation of spatial patterns in total egg and larval concentrations and interpolate the discrete station data, spatial distribution of total eggs and larvae were contoured using linear kriging in Surfer 7.0 (Golden Software, Golden, Colorado). This contouring allowed interpolation between stations, smoothed variability inherent in ichthyoplankton sampling, and provided a comprehensive and easily interpretable plot of spatial variability.

## Results

### Ichthyoplankton

Temporal peaks in eggs and larvae varied considerably among taxa (Tables 1, 2), but total concentrations of eggs and larvae were highest in August during the 3 years sampled (Fig. 2). Although high numbers of eggs were observed in the spring and summer, larval numbers were low except during August and September. We also observed differences in the timing of egg production among species. Early stage Atlantic cod egg abundance was high in April and June of all years and began to decline by August (Fig. 3; Bradbury et al. 2000). A similar pattern was observed in American plaice, *Hippoglossoides platessoides*, but for both of these taxa late-stage eggs were much more abundant in the August and September sampling periods (Fig. 3). Early stage eggs of cunner – yellowtail flounder were abundant in June but peaked in August; late stages were again abundant in August and September. Early stages of fourbeard rockling were abundant in June and September, whereas late stages were most abundant in August and September.

Temporal patterns in larval concentrations of pelagic spawners were consistent with patterns in late-stage eggs (Fig. 4). Atlantic cod, American plaice, cunner, yellowtail flounder, witch flounder, and fourbeard rockling were all most abundant in the August and September sampling periods and were uncommon in April through June, despite the fact that egg production in some of these taxa peaked during those time periods.

Temporal patterns in the dominant taxa of bottom spawners were markedly different than those of pelagic spawners. With the exception of capelin, *Mallotus villosus*, where larval concentrations peaked in August and September, larval production in all the dominant taxa of bottom spawners peaked before or during June (Fig. 5). Larvae of bottom spawners were also present over a wider sampling period than those of pelagic spawners; the latter were rarely observed before August, whereas the former were abundant from April through June. Larval sizes also varied over time; mean larval size was larger for most taxa during the earlier sampling periods than during later surveys and coincided with a change in species composition from larvae predominantly of bottom spawners to those of pelagic spawners (Fig. 6).

Distributions of stage I eggs of pelagic spawners, which provide an indication of spawning location, suggest that

**Fig. 2.** Concentrations of eggs and larvae averaged for each sampling trip over the entire sampling area for (*a*) 1997, (*b*) 1998, and (*c*) 1999. Solid bars denote pelagic-spawner eggs, light shaded bars denote pelagic-spawner larvae, open bars denote bottom-spawner larvae, and hatched bars denote bottom-spawner larvae excluding capelin (*Mallotus villosus*). Error bars denote 1 standard error.

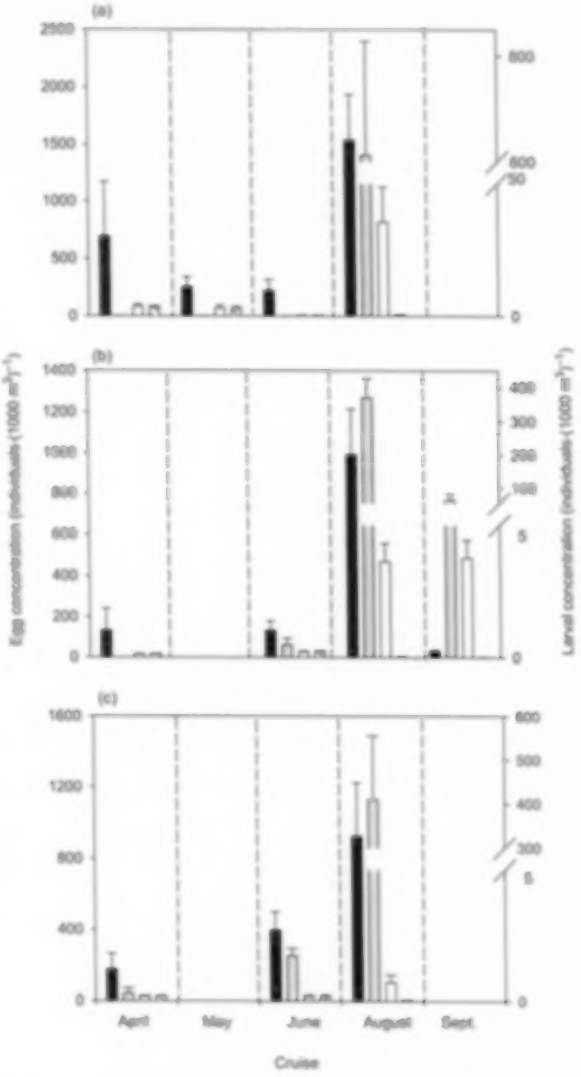


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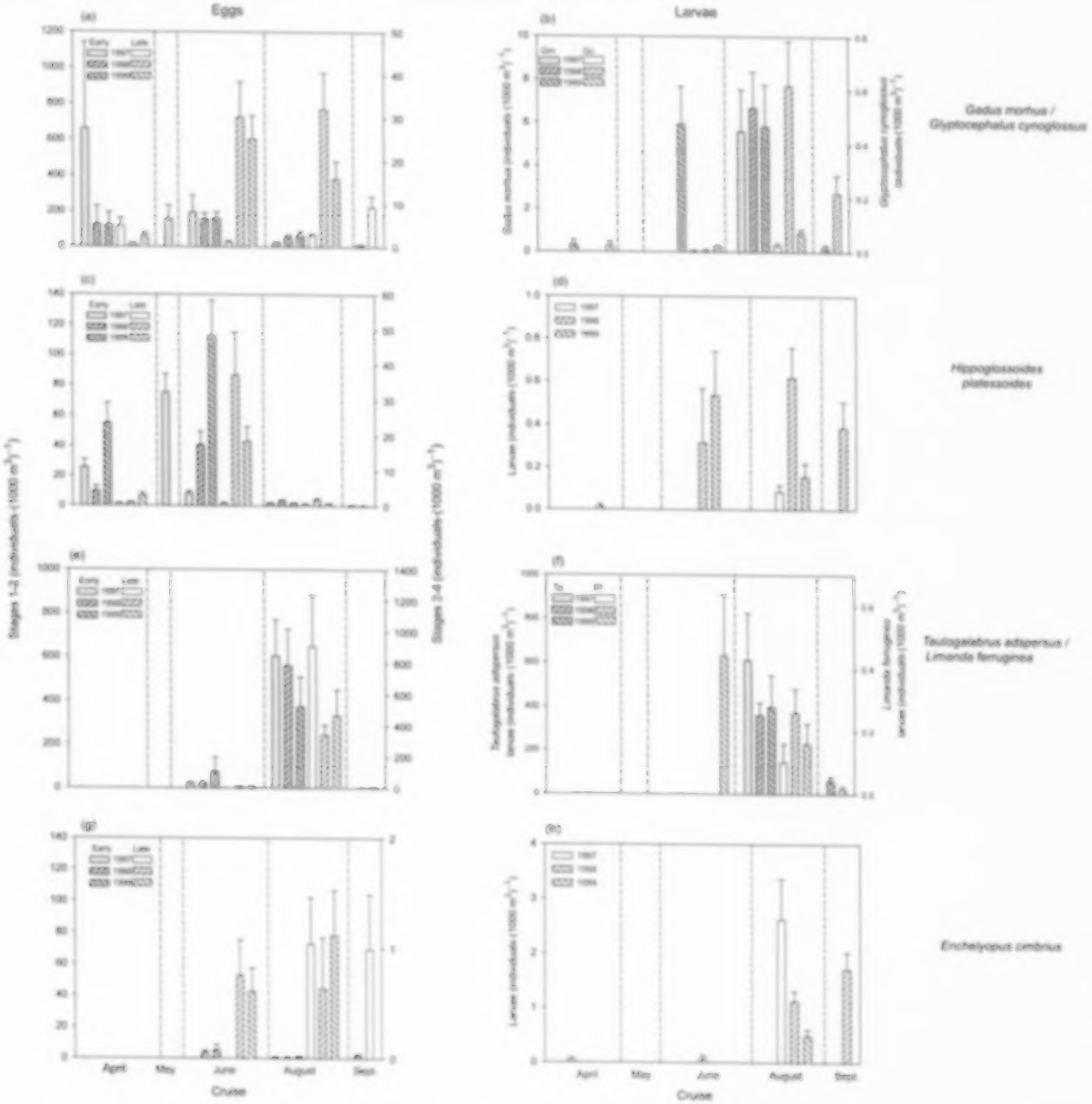
**Fig. 3.** Mean concentrations of early and late egg stages and larvae for pelagic spawners during each sampling trip in each year of sampling for (*a*) Atlantic cod (*Gadus morhua*) – haddock (*Melanogrammus aeglifinus*) – witch flounder (*Glyptocephalus cynoglossus*) eggs, (*b*) Atlantic cod – witch flounder larvae, (*c*) American plaice (*Hippoglossoides platessoides*) eggs, (*d*) American plaice larvae, (*e*) cunner (*Tautogalabrus adspersus*) – yellowtail flounder (*Limanda ferruginea*) eggs, (*f*) cunner – yellowtail flounder larvae, (*g*) fourbeard rockling (*Enchelyopus cimbrius*) – hakes eggs, (*h*) fourbeard rockling larvae.




some taxa utilize the same areas of the bay repeatedly over time. Concentrations of early stage Atlantic cod (Fig. 7) and fourbeard rockling (Fig. 8) were typically highest near the head of the bay, although fourbeard rockling eggs were also abundant along the eastern side. Early-stage American plaice (Fig. 9) and cunner – yellowtail flounder eggs (Fig. 10) were typically most abundant along the western side of the bay, though both were abundant along the eastern side as well. For all these taxa, peak abundance was at the head or on the western side of the bay.

Larval concentrations for these pelagic spawning taxa were negligible until August, when the vast majority of larvae occurred at the head or along the western side of the bay (Figs. 7–10). The spatial coherence among larvae of pelagic

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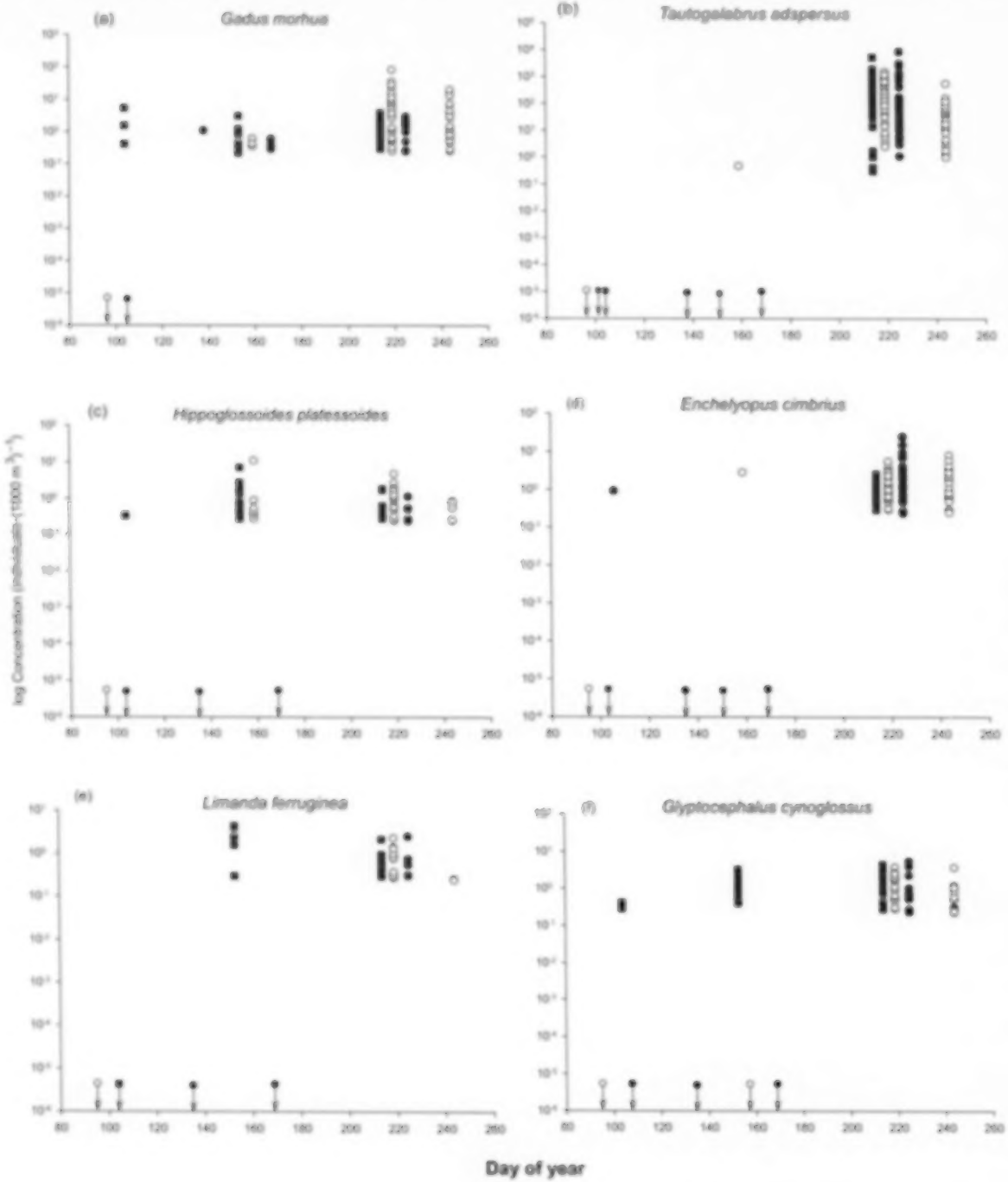
**Fig. 4.** Concentrations of larvae of dominant species of pelagic spawners at all stations sampled for 1997 (solid circles), 1998 (open circles), and 1999 (solid squares). Arrows above horizontal axes indicate sampling times where no individuals were collected at any stations.




spawners was much greater than that observed in bottom spawners, which varied spatially among species (P. Snelgrove, I. Bradbury, and S. Fraser, unpublished data). The linkage between presumed spawning location and advection for pelagic spawners was generally consistent in August, in that peak numbers in eggs and larvae were in similar areas of the bay in

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**Fig. 5.** Concentrations of larvae of dominant species of bottom spawners at all stations sampled for 1997 (solid circles), 1998 (open circles), and 1999 (solid squares). Arrows above horizontal axes indicate sampling times where no individuals were collected at any stations.

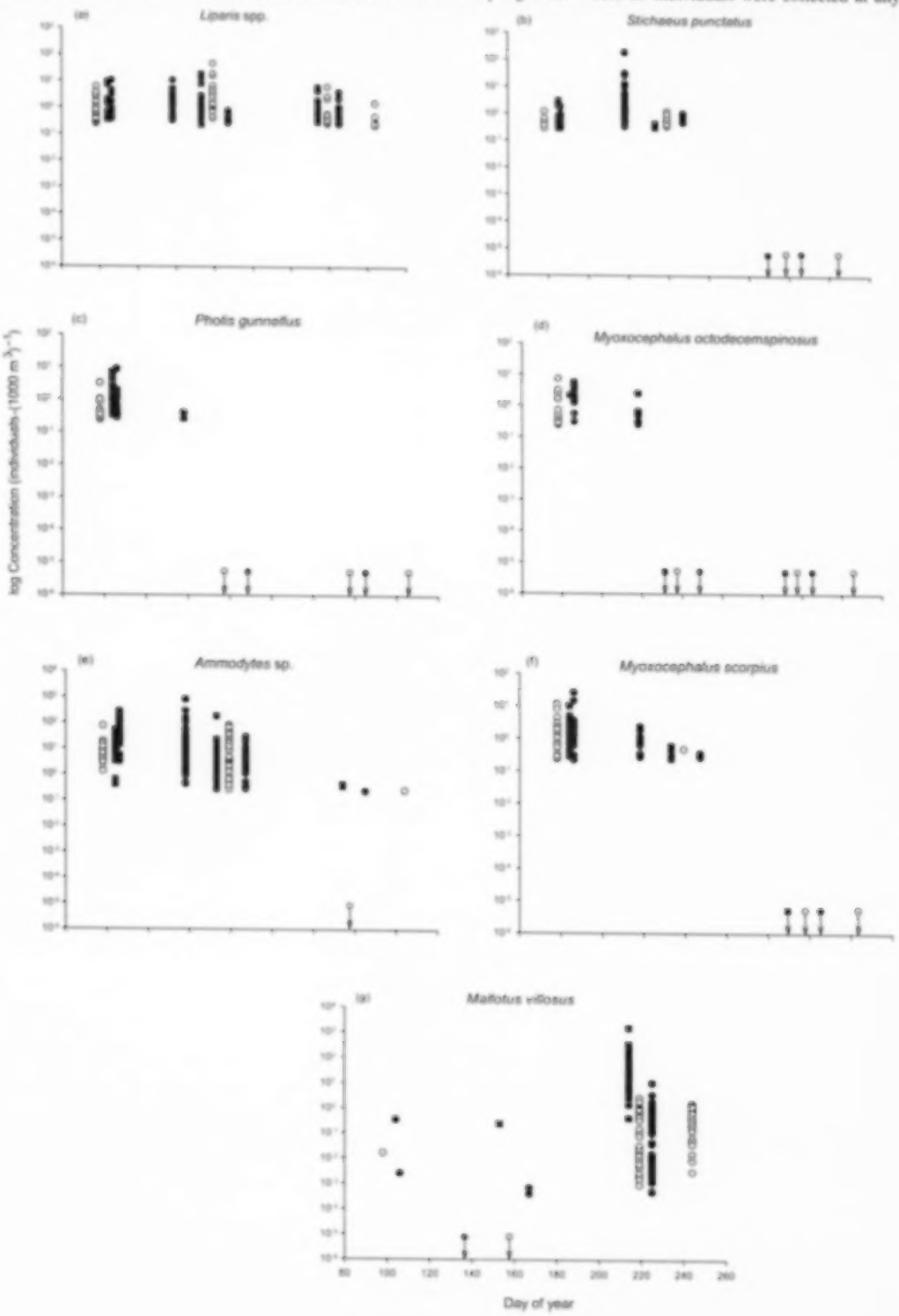


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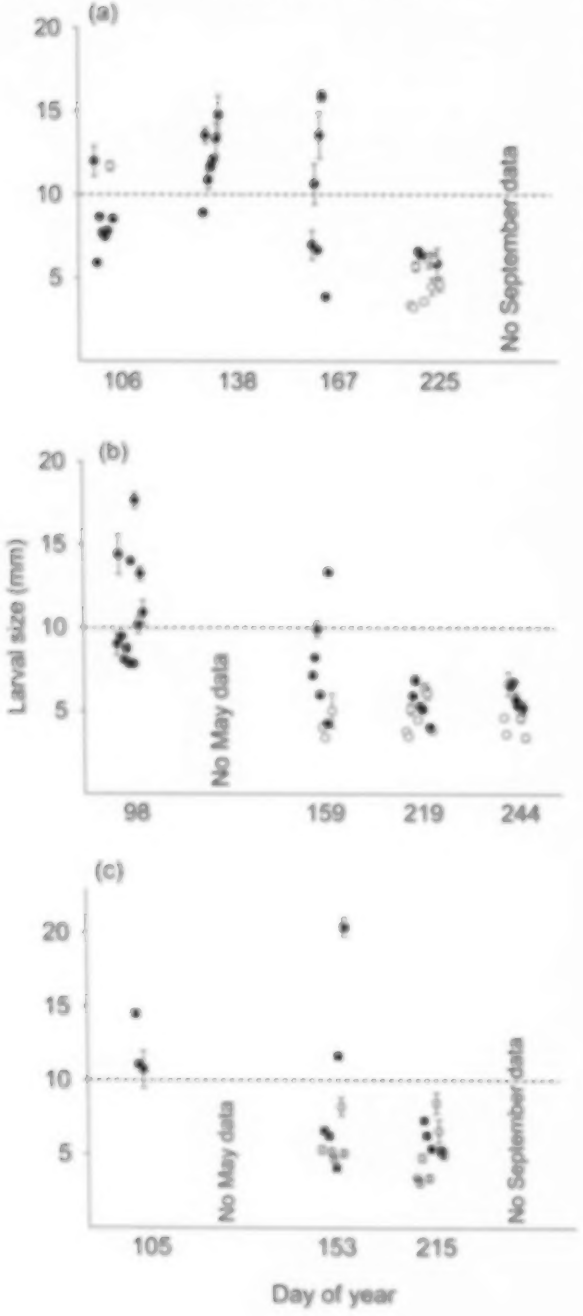
**Fig. 6.** Station means of larval size for each taxon for which more than five individuals were collected within a given sampling trip. Lines around points denote 1 standard error. Open points denote larvae from pelagic spawners; solid points denote larvae from bottom spawners. (*a*) 1997, (*b*) 1998, (*c*) 1999. Broken horizontal line indicates the 10 mm threshold identified by Bradbury et al. (2003) as a developmental stage where swimming ability is sufficient to contribute substantially to larval distributions.




all years. August was the only time when late stages and larvae were abundant. Early stages were typically most abundant near the head of the bay, whereas late stages were concentrated along the western side toward the outer part of the bay (Figs. 7–10).

### Environmental data

Mixed-layer temperatures at the head of the bay or averaged over the full bay in April were 0–1 °C (Fig. 11) and showed little spatial variability. By August, mixed-layer temperatures were typically 6–9 °C with corresponding surface temperatures of 13–17 °C. The head and outer southeast parts of the bay were generally warmest, whereas the coolest area was the southwest side where upwelling was observed (P. Snelgrove, I. Bradbury, and S. Fraser, unpublished data). Chlorophyll in the bay exhibited considerable temporal and spatial variability. High concentrations of chlorophyll were observed in April and September. In terms of spatial variability, the center and outer areas of the bay were typically lowest in chlorophyll, whereas highest values were observed at the head of the bay and along the western side (Bradbury et al. 2000), as was also observed with zooplankton (Fig. 12). SeaWiFs images were consistent with our estimates based on chlorophyll extraction (Bradbury et al. 2000). Zooplankton abundance was highest in August and lowest in June (Fig. 12), and within-cruise spatial variability in abundance was also highest in August when the hydrographic structuring of the bay was strongest (Bradbury et al. 2000). As with phytoplankton, highest zooplankton abundances were observed on the western side of the bay, where, in August, larvae were most concentrated.

## Discussion

Placentia Bay ichthyoplankton display strong temporal variability in abundance that is related to spawning strategy, advection, and areas of elevated production. For pelagic spawners in particular, it is likely that the strong directional flow observed in Placentia Bay creates a retention problem that is strongest when water temperatures are low. In open systems, or bays with strong directional flow, transport out of a suitable environment is more likely to occur during cooler periods when egg and larval development rates are slow (e.g., Pepin 1991). In gyre systems (e.g., O'Boyle et al. 1984; Werner et al. 1993), where flushing is less of an issue, egg development time creates less of a constraint. This flushing problem is particularly exacerbated in areas with very short development seasons (Conover 1992). Placentia Bay is a complex spawning environment not only because of the directional flow, but also because of the short period when water temperatures are warm. Although substantial numbers of pelagic eggs were spawned in the spring by several taxa, late-stage eggs and hatched larvae were rare or completely absent until late in the summer, suggesting that they were flushed from Placentia Bay and (or) experienced high rates of mortality. Larvae of bottom spawners, by contrast, were abundant in April through August and were found over a broader geographic area than larvae from pelagic spawners. Thus, timing and spatial distributions of larvae for bottom spawners, in which developing eggs are affixed to the bottom, may be less influenced by water temperature,

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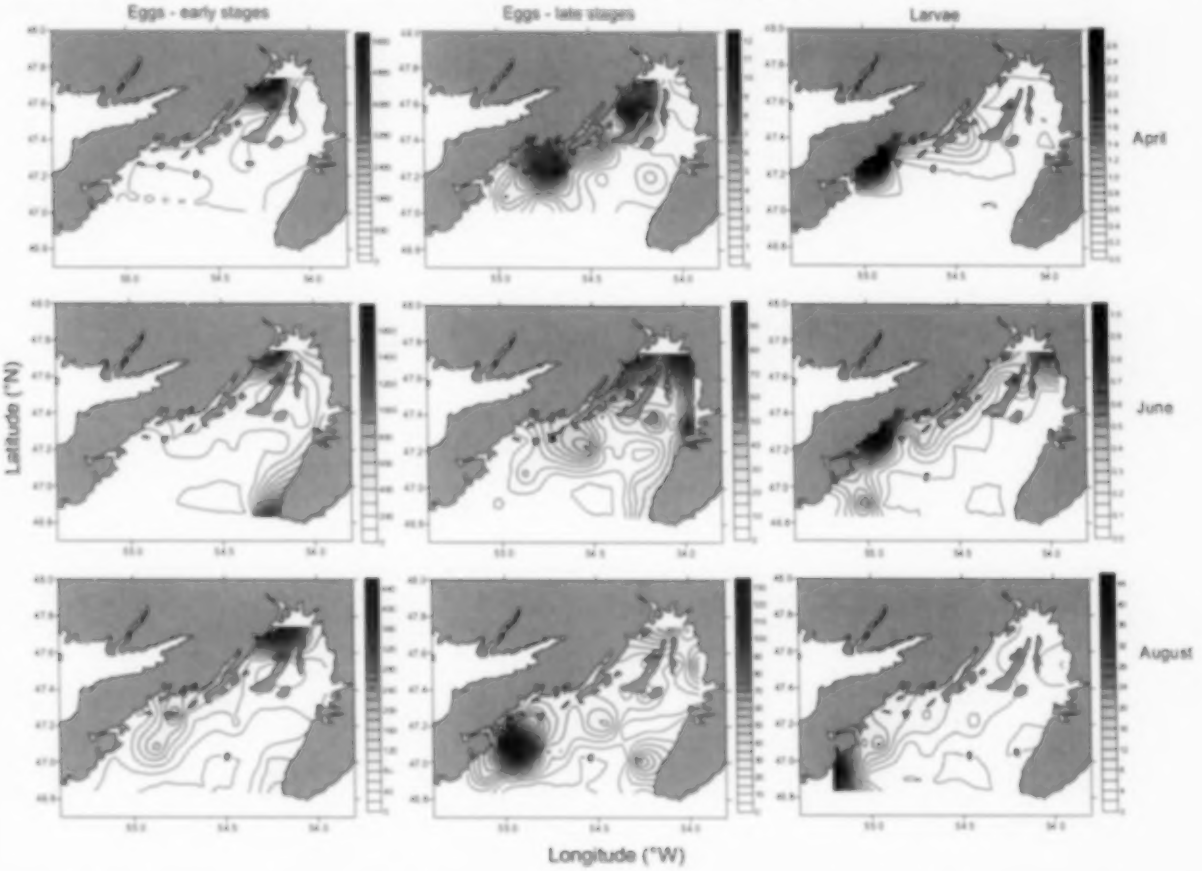
**Fig. 7.** Linear kriging plots of concentrations (individuals·(1000 $m^3$)$^{-1}$) of early- and late-stage eggs and larvae of Atlantic cod (*Gadus morhua*) for April, June, and August cruises 1997–1999. Note change in scale among panels.




flushing, and temperature-dependent mortality. Larvae of both types of spawners were associated with times and locations of high zooplankton abundance, suggesting that food availability may also play a role in seasonal and spatial dynamics.

## Flushing rates for Placentia Bay

The mean circulation in Placentia Bay is influenced by inflow of the inshore branch of the Labrador Current and wind forcing. The cold Labrador Current water is carried around the Avalon Peninsula in a deep nearshore channel (Petrie and Anderson 1983) and enters on the eastern side of Placentia Bay, where it is the primary forcing term that generates the strong, mean counterclockwise circulation of the near-surface waters (Schillinger et al. 2000). The water has the characteristics of the Labrador Current in that it is relatively cold and fresh with a well-understood, depth-dependent seasonal cycle (Petrie et al. 1991). Studies of the coastal embayments on the northern side of the Avalon Peninsula (cf. deYoung and Sanderson 1995; Davidson et al. 2001) have shown that Trinity Bay, which is similar in scale to Placentia Bay, has a similarly well-developed mean circulation, whereas Conception Bay, which is substantially smaller, lacks a well-defined mean circulation (deYoung and Sanderson 1995).

The near-surface mean currents in Placentia Bay are roughly 10–12 cm·$s^{-1}$ at 20 m depth (Schillinger et al. 2000). These current measurements were made during the summer, from May to September, during the same period as for the egg and larval surveys. Although the calculation of mean residence time should consider the influence of wind forcing (e.g., deYoung et al. 1994, for Conception Bay), the much greater strength of the mean current in Placentia Bay allows a reasonable analysis for transport times through the bay based on circulation data. Considering the length of Placentia Bay to be about 120 km and taking a mean transport of 10 cm·$s^{-1}$ (based on measurements from the four quadrants of the bay) yields an along-bay transport of 14 days and a similar time for transport out of the bay on the western side. Thus, the total time of transit for eggs or larvae that are released in the surface water near the mouth on the eastern side of the bay would be roughly 28 days.

## Pelagic egg development times and transport

Given that the approximate flushing time from the head of the bay to the southwest extremity of the bay is ~14 days and the complete flushing time from the southeast extremity to the southwest extremity is ~28 days, there are important im-

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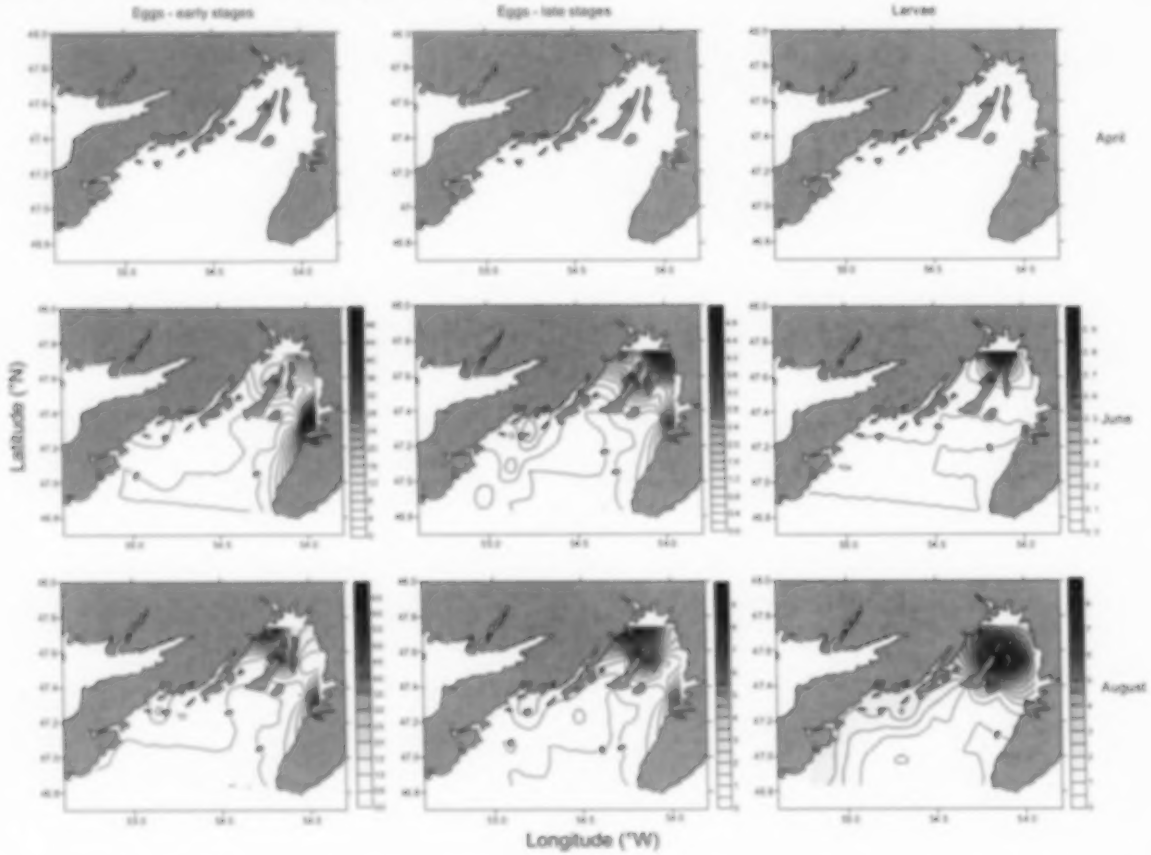
**Fig. 8.** Linear kriging plots of concentrations (individuals·(1000 $m^3$)$^{-1}$) of early and late stage eggs of fourbeard rockling (*Enchelyopus cimbrius*) and larvae for April, June, and August cruises 1997–1999.




plications for pelagic egg loss as a function of temperature-dependent development rate. Simple modeling of Atlantic cod development rates suggests that in April, hatch may not occur for as long as 41 days, whereas in August this time is reduced to ~8 days (Bradbury et al. 2001). Both American plaice and Atlantic cod produce substantial numbers of eggs in April (and to some extent June) near the head of the bay when water temperatures are comparatively low. These eggs were likely spawned near the head of the bay given that cod are known in that area in spring (Lawson and Rose 2000), and in both species the eggs are predominantly stage 1. Based on flushing time estimates outlined above, there is a strong likelihood that during spring, when water temperature are ~1 °C, the eggs would be flushed from the bay prior to hatching. The low numbers of late-stage eggs and larvae in April are consistent with this interpretation. The other common pelagic spawners, fourbeard rockling and cunner – yellowtail flounder, were absent in April, but early stages through late stages were present in low numbers in June. During June, fourbeard rockling showed a progression of stages from the head of the bay towards the southwest.

In August, when water temperatures were warmest, larvae and late-stage eggs of pelagic spawners were most abundant, and concentrations were often highest "downstream" of sites along the western side and head of the bay, where early stages were most abundant.

Temperature and wind were both found to be critical factors in the timing of spawning for pelagic and bottom spawners in Conception Bay (Laprise and Pepin 1995), which is just north of Placentia Bay. Given the similarity in temporal patterns in Placentia Bay in 1997, 1998, and 1999, our data are consistent with this interpretation, but spawning strategy also plays a key role.

## Larval growth and swimming

Warmer temperatures not only decrease egg development time but also increase larval growth (Pepin 1991), thereby providing a double advantage to late summer spawning by pelagic species. Thresher (1984) noted that recently hatched larvae from pelagic eggs have undeveloped fins and unpigmented eyes that may make them more vulnerable to dispersal than larvae from bottom spawners (see Suthers and Frank 1991), so that largely passive transport is an issue for recently hatched pelagic larvae as well as for eggs. Our size data suggest that larvae from pelagic spawners were indeed typically much smaller than those produced by bottom spawners. Thus, although the same spawning sites were often used throughout extended periods by pelagic spawners,

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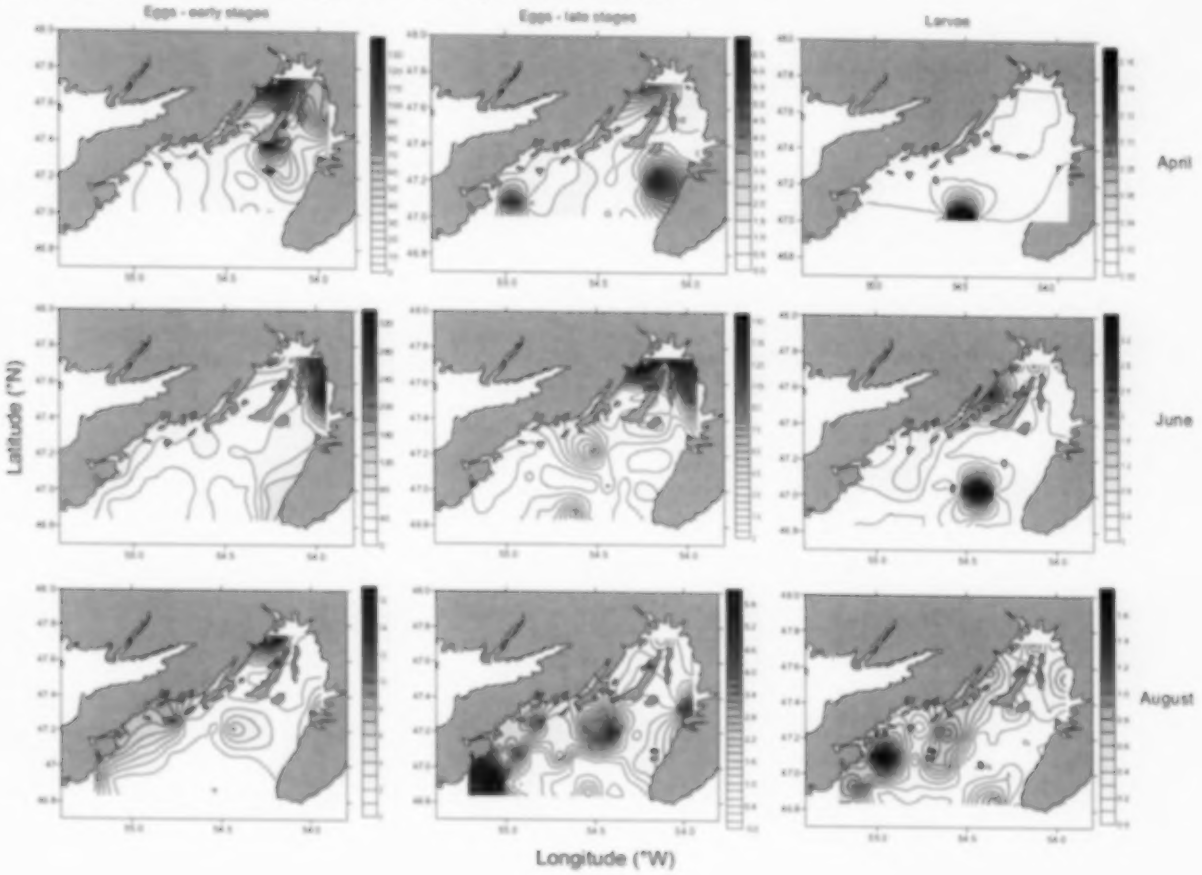
**Fig. 9.** Linear kriging plots of concentrations (individuals·(1000 $m^3$)$^{-1}$) of early- and late-stage eggs and larvae of American plaice (*Hippoglossoides platessoides* for April, June, and August cruises 1997–1999.




successful development and hatching within the bay was largely a late summer phenomenon.

### Zooplankton availability

Total zooplankton abundance was highest in August, with highest concentrations typically found at the head of the bay. Thus, in terms of spatial pattern, the spawning strategy for pelagic taxa was appropriate for placing hatching larvae in a food-rich environment (e.g., Hjort 1914; Cushing 1990). In fact, total pelagic egg concentrations were highest in August at a time when development times were shortest. Nonetheless, high levels of spring egg production in some taxa (Atlantic cod, American plaice) may have resulted in flushing and (or) high rates of mortality, given the low numbers of late-stage eggs and larvae prior to August.

Not all pelagic spawners utilized the same strategy with respect to timing. Some species (fourbeard rockling, cunner, yellowtail flounder) spawn so that peak concentrations occur in August, whereas other taxa (Atlantic cod, American plaice) spawn over a broader period when food availability and temperature change considerably (see Hutchings and Myers (1994) for discussion on variability in cod spawning). The variability in timing of peak copepod abundance that has been described for the broader area of the North Atlantic may be a contributing factor to this variability. Thus, different species utilize different strategies with respect to timing (Sherman et al. 1984), with different degrees of bet-hedging. Sherman et al. (1984) noted widespread larval distribution for some taxa and suggested that species such as Atlantic cod may adhere to tighter spawning locations to match larvae spatially to available food. Spawning upstream of productive areas by cod had been noted by other authors (e.g., Munk et al. 1995), as has association of high egg concentrations in areas with high zooplankton abundance (Doyle and Ryan 1989; P. Snelgrove, I. Bradbury, and S. Fraser, unpublished data). Indeed, many studies have proposed downstream drift by larvae to appropriate nursery grounds (Harden Jones 1969; deYoung and Rose 1993).

### Bottom spawners

Unlike pelagic species, peaks in larval abundance of bottom-spawning species were highest in spring and early summer (with the notable exception of capelin). Because larvae of bottom spawners have a greater capacity to regulate their distribution than pelagic eggs or recently hatched larvae (Thresher 1984) and can begin feeding soon after they

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**Fig. 10.** Linear kriging plots of concentrations (individuals·(1000 $m^3$)$^{-1}$) of cunner (*Tautogolabrus adspersus*) – yellowtail flounder (*Limanda ferruginea*) early- and late-stage eggs and cunner larvae for April, June, and August cruises 1997–1999. Note the differences in scale among plots.

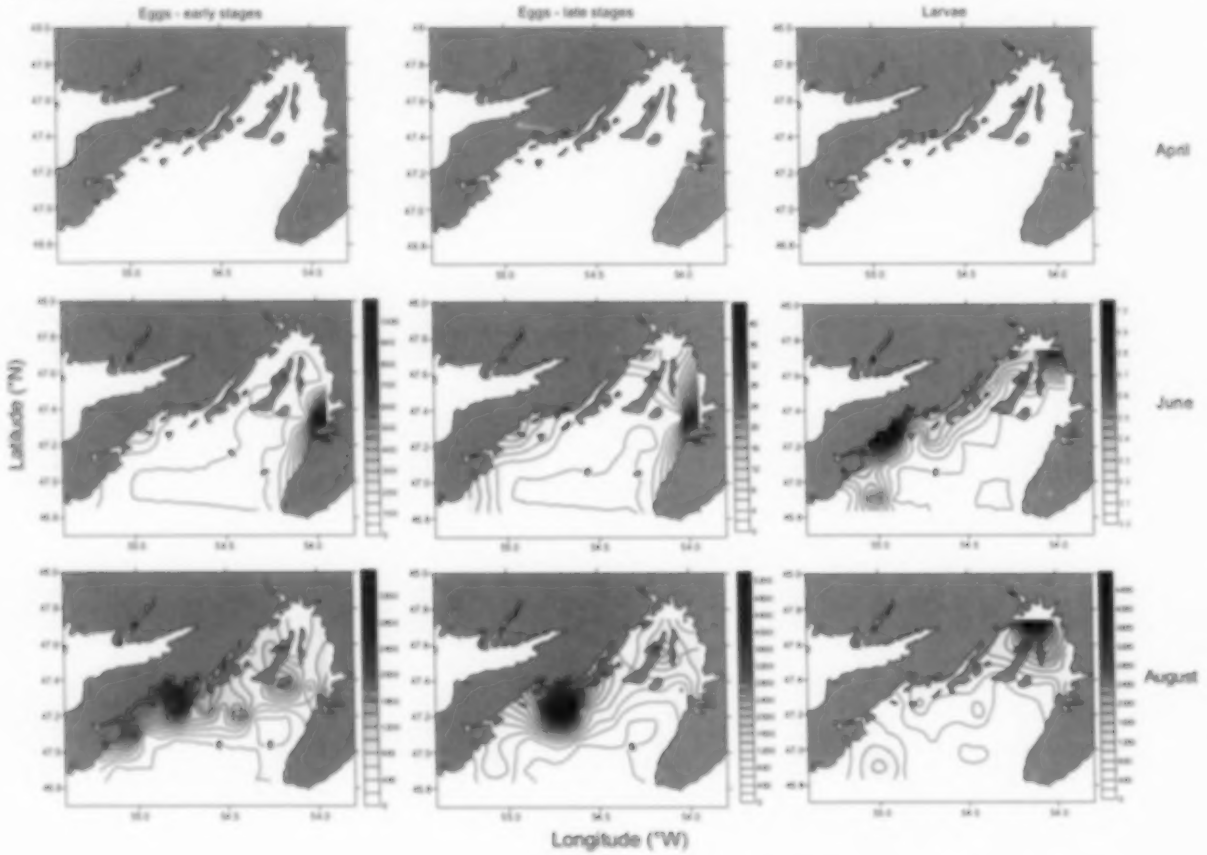
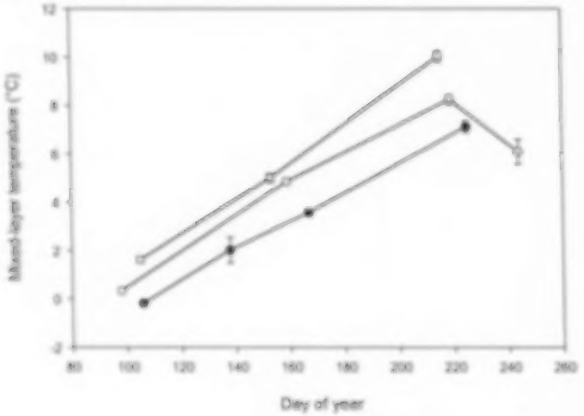



**Fig. 11.** Mean mixed-layer temperatures averaged for all stations during each cruise in 1997 (solid circles), 1998 (open circles), and 1999 (open squares).




are planktonic, their vulnerability to flushing in cold water is greatly reduced. For example, swim speeds of recently hatched Atlantic cod larvae are only 1.18 cm·$s^{-1}$, whereas those of recently hatched shorthorn sculpin, *Myoxocephalus scorpius*, are 5.56 cm·$s^{-1}$ (Guan 2007). Moreover, our size data suggests that the larvae produced by bottom spawners in spring were larger than the larvae collected later in the year. We have argued elsewhere, based on scaling and changes in patch size with larval development (Bradbury et al. 2003), that 10 mm represents a critical size transition for fish larvae; individuals larger than this threshold have sufficient swimming capacity to contribute considerably to their distribution. Those larvae that were present in spring were near or above this size threshold, whereas those present in summer were almost invariably much smaller. The spring bloom in Placentia Bay results in high abundances of zooplankton; larvae hatching in spring may therefore be able to utilize some of these food resources. Because zooplankton are also abundant over a broader area in April than in August, larvae from bottom spawners may not face the same constraint of having to place hatching larvae in a particular area of the bay. The greater swimming ability and reduced

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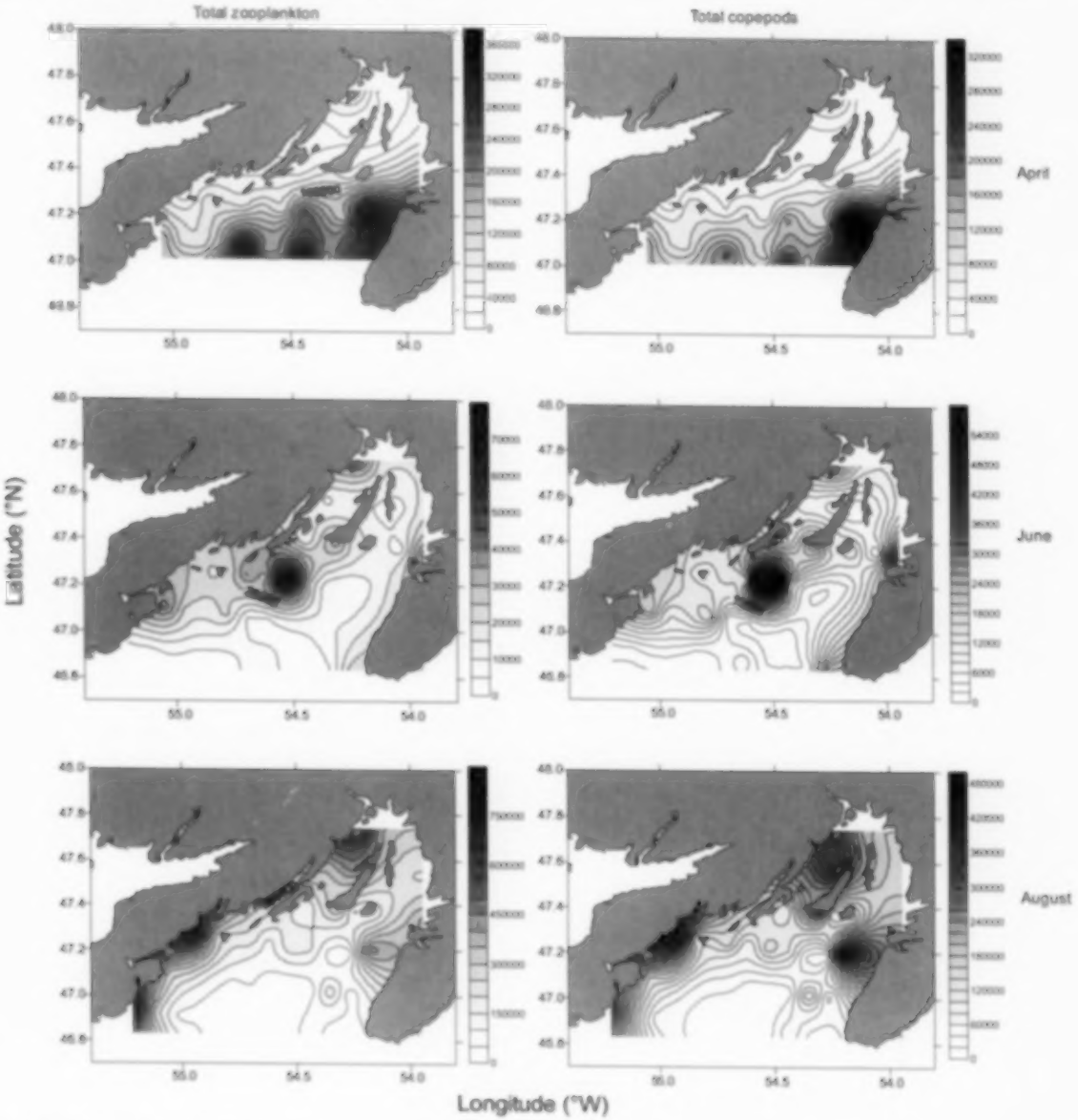
**Fig. 12.** Linear kriging plots of average total zooplankton abundance (individuals·(1000 $m^3$)$^{-1}$) for April, June, and August cruises 1997–1999. Note the differences in scale among plots.




dependence of larvae of bottom spawners on specific areas of the bay may also explain why they are present over a broader time period than pelagic larvae, which are heavily concentrated in the August sampling period. Larval patterns of bottom-spawning species are therefore dictated more by availability of suitable spawning habitat than by physical transport or peak zooplankton concentrations (P. Snelgrove, I. Bradbury, and S. Fraser, unpublished data). Temperature is thought to be a key factor in terms of emergence of bottom-spawned larvae (Frank and Leggett 1983) and may explain the temporal synchrony among most species. *Mallotus villosus*, the only bottom spawner with a late summer larval peak, has shown unseasonably late spawning in recent years (Carscadden et al. 2001).

In conclusion, different taxa use different spawning strategies in the strongly seasonal Placentia Bay environment. Some pelagic spawners release eggs over a broad time period from spring through fall, resulting in advective loss or high mortality in the spring and greater hatching success in late summer. Other pelagic spawners are more confined to the late summer, when temperatures are more favourable for rapid egg and larval development. Pelagic spawning often

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occurs coincident with or upstream of the most productive areas of the bay, and larval abundance peaks when zooplankton are most abundant. Larvae of bottom spawners typically emerge in the spring, likely reflecting the superior swimming ability of larvae that have hatched from bottom-spawned eggs and allowing them to take advantage of zooplankton associated with the spring bloom.

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# Estimating abundance of spatially aggregated populations: comparing adaptive sampling with other survey designs

**Kathryn L. Mier and Susan J. Picquelle**

**Abstract:** The main goal in estimating population abundance is to maximize its accuracy and precision. This is difficult when the survey area is large and resources are limited. We implemented a feasible adaptive sampling survey applied to an aggregated population in a marine environment and compared its performance with five classical survey designs. Specifically, larval walleye pollock (*Theragra chalcogramma*) in the Gulf of Alaska was used as an example of a widespread aggregated population. The six sampling designs included (*i*) adaptive cluster, (*ii*) simple random, (*iii*) systematic, (*iv*) systematic cluster, (*v*) stratified systematic, and (*vi*) unequal probability. Of the five different adaptive estimators used for the adaptive cluster design, the modified Hansen–Hurwitz performed best overall. Of the six survey designs, the stratified systematic survey provided the best overall estimator, given there was accurate prior information on which to base the strata. If no prior information was available, a systematic survey was best. A systematic survey using a single random starting point with a simple random estimator performed as well as and sometimes better than a systematic cluster survey with two starting points (clusters). The adaptive cluster survey showed no advantages when compared with these two designs and furthermore presented substantial logistical challenges.

**Résumé :** L'objectif principal poursuivi dans l'estimation de l'abondance d'une population est l'amélioration de l'exactitude et de la précision. Cela est difficile quand la surface inventoriée est grande et les ressources limitées. Nous avons mis au point un inventaire adaptatif d'échantillonnage pratique pour une population à distribution contagieuse dans un environnement marin et nous avons comparé sa performance en fonction de cinq plans d'inventaire classiques. Nous utilisons, en fait, des larves de goberges (*Theragra chalcogramma*) de l'Alaska du golfe de l'Alaska comme exemple spécifique d'une population à large répartition et à distribution contagieuse. Les six plans d'inventaire consistent en (*i*) un plan adaptatif avec regroupements, (*ii*) un plan aléatoire simple, (*iii*) un plan systématique, (*iv*) un plan systématique avec regroupements, (*v*) un plan systématique stratifié et (*vi*) un plan à probabilités inégales. Des cinq estimateurs adaptatifs utilisés dans le plan adaptatif avec regroupements, l'estimateur modifié de Hansen–Hurwitz donne le meilleur résultat global. Des six plans d'inventaire, l'inventaire systémique stratifié fournit le meilleur estimateur global, étant donné qu'il existe de l'information préalable précise pour déterminer les strates. Lorsqu'il n'y a pas de renseignements préalables, l'inventaire systématique fonctionne le mieux. Un inventaire systématique avec un seul point de départ aléatoire et avec un estimateur aléatoire simple fonctionne aussi bien, et souvent mieux, qu'un inventaire systématique avec regroupements avec deux points de départ (regroupements). L'inventaire adaptatif avec regroupements ne présente aucun avantage par rapport aux deux plans précédents et, de plus, il crée de sérieux problèmes de logistique.

[Traduit par la Rédaction]

## Introduction

The most common requirement in resource management, studies of population dynamics, and many other subjects is to estimate mean abundance of spatially aggregated populations. The usefulness of these estimates are dependent on their bias and precision. Yet, in most field studies, traditional survey procedures are used without much background information on how to improve the bias and precision of the mean and standard error estimators. This can lead to inaccurate fish stock assessments or hypothesis tests and general misrepresentation of the spatial distribution.

The goal of this project was to compare the effectiveness of six sampling methods on patchy distributions (i.e., adaptive cluster, random, systematic, systematic cluster, stratified systematic, and unequal probability). The criteria for comparing designs were the bias, precision, and mean squared error (MSE) of the estimates. Because MSE is a measure of

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both bias and precision, it was used as a final criterion for determining the best estimator. We computed these estimates of the mean density and their standard error (SE) by simulating many patchily distributed populations with different degrees of patchiness and then repeatedly sampling these populations using each sampling method.

A primary motivation for this study was to decide if using an adaptive cluster design (Thompson 1990) would yield a more precise estimate. This design has received much attention in recent years with studies of patchily distributed populations, primarily because it allows concentrated sampling around initial samples that meet a predetermined criterion (typically areas of high density) and because it is reported to yield a smaller variance than random sampling. It can be particularly useful when more individuals of interest need to be collected for other studies.

In our study, we examine the performance of adaptive cluster sampling by sampling from realistic, simulated populations. Other examples of adaptive sampling applied to simulated patchily distributed populations include Christman (2000), Brown (2003), and Su and Quinn (2003). Christman (2000) looked at adaptive cluster sampling of rare, spatially clustered populations. In contrast, our population of interest is patchy or clustered, but not rare, and covers a large geographic extent. Our simulated populations are typical of many ubiquitous but patchy marine species, such as adult Pacific hake (*Merluccius productus*) and shortspine thornyhead (*Sebastolobus alascanus*) along the west coast of North America, adult arrowtooth flounder (*Atheresthes stomias*), rex sole (*Glyptocephalus zachirus*), and Pacific sandlance (*Ammodytes hexapterus*) in the Gulf of Alaska, and many species of ichthyoplankton; hence, our survey design comparisons have broad applicability. To further broaden the scope of our study, we simulated populations with a wide range of patchiness.

What also sets our paper apart from other simulations is the focus on a realistic implementation of an adaptive sampling design where the sampling unit is extremely small when compared with the entire area to be surveyed, a scenario that is common in large marine surveys. Our simulated population contained almost 9000 sampling units, whereas, for example, Thompson (1991) used a population with 400 sampling units, and Christman (2000) used a population with 75 sampling units. Our implementation includes setting the criterion for initiating adaptive sampling, controlling sample size, and avoiding negative variance estimates (which occurs in Horvitz–Thompson estimates). These issues have not been adequately addressed in real applications or in simulated samples. Much of the literature a priori uses species presence to initiate adaptive sampling, makes no attempt to control sample size, and seldom yields negative variances due to artificially simple populations. Those studies that have introduced methods to control sample size include Lo et al. (1997), Christman (2003), and Su and Quinn (2003). Each of these methods introduces bias into the estimator, as does our method. We measured the bias, or systematic error, by simulating realistic populations and then repeatedly sampling from these populations and comparing the true values to the repeated estimates.

Common estimators used for adaptive cluster sampling include the modified Hansen–Hurwitz (HH) and Horvitz–Thompson (HT) estimators of the mean and variance (Thompson and Seber 1996). In addition to these two, we also looked at two alternate estimators of the variance of the HT mean, the Yates–Grundy–Sen (Sen 1953; Yates and Grundy 1953) and the Brewer–Hanif (Brewer and Hanif 1983), as well as one other estimator of both the mean and variance, the Hajek–Sarndal (Hajek 1971; Sarndal et al. 1992). Patchy distributions usually yield large variances, regardless of survey design (Andrew and Mapstone 1987), but several studies suggest that using the modified HT estimator in an adaptive cluster survey yields the most precise estimate (Hanselman et al. 2003; Salehi 2003; Su and Quinn 2003). These conclusions, however, were dependent on the degree of aggregation, "neighborhood" definition, size of "networks", within-network variance, size of "initial sample", size of "sampling unit", and the "criterion" used to begin adaptive sampling (see Appendix A for definitions of terms that are in quotes).

We apply these methods to estimating mean density (number per 10 $m^2$) of larval fish in the ocean, and specifically to the patchily distributed walleye pollock (*Theragra chalcogramma*) (Stabeno et al. 1996). We patterned our simulated populations on the distribution of walleye pollock larvae as recorded from ichthyoplankton surveys in Shelikof Strait, Alaska, conducted by the National Oceanic and Atmospheric Administration (NOAA) Alaska Fisheries Science Center (AFSC). We built the framework used in this study by modeling the spatial distribution in terms of patches and using parameters that describe these patches based on actual historical data.

## Materials and methods

### Population simulations

Artificial populations were generated that have the same spatial characteristics as walleye pollock larvae in early May in Shelikof Strait, Alaska. The primary characteristic is the spatial pattern of its patches, that is, areas of high density (Stabeno et al. 1996). We examined the observed larval walleye pollock spatial distributions from nine spring ichthyoplankton surveys conducted by AFSC between 1986 and 1998 (Table 1). We chose surveys from the time interval shortly after the eggs hatched into larvae and before the larvae became widely dispersed, so that the patches were still coherent.

To examine the effect of patchiness on the performance of the various survey designs, we simulated two sets of populations: 50 populations that we considered to be very patchy and 50 populations that were much less patchy. We defined high-patchy populations to have patches that were small in geographic extent, but had large maximum densities within the patch. Conversely, we defined low-patchy populations to have patches that were large in geographic extent, but with maximum densities that were less extreme than the high-patchy population (Fig. 1). We adopted these definitions both because they are intuitive and because Brown (1996) found that these factors (along with the number of patches) were the most important in determining the benefits of adap-

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**Table 1.** List of cruises used to describe spatial distribution of larval walleye pollock (*Theragra chalcogramma*).

| Cruise | Dates | No. of stations |
|---|---|---|
| 2MF86 | 4–17 May 1986 | 89 |
| 2MF89 | 26 April – 2 May 1989 | 45 |
| 3MF89 | 9–16 May 1989 | 94 |
| 2MF90 | 8–13 May 1990 | 51 |
| 3MF92 | 3–9 May 1992 | 64 |
| 4MF93 | 6–11 May 1993 | 66 |
| 5MF94 | 5–8 May 1994 | 50 |
| 1DF96 | 30 April – 5 May 1996 | 73 |
| 4MF98 | 3–5 May 1998 | 45 |

tive sampling over random sampling. By simulating populations with a wide range of patchiness, the conclusions drawn from these populations may be extrapolated to many other natural populations that have various degrees of patchiness.

The area of the simulated populations was defined by plotting the stations from cruises in Table 1 and delineating the area that was usually surveyed and contained larvae (Fig. 2). A grid of 8857 "cells", where each cell is 1 nautical mile × 1 nautical mile (1 n.mi. = 1.852 km) sea-surface area, was created inside this survey area. A density was simulated for each cell based on patch parameters estimated from historical data. This density was defined as the number of fish in the water column below a 10 $m^2$ surface area within the cell. We used the index $i$ to refer to the $i$th cell; $x_i$ and $y_i$ to refer to the east–west and north–south location of the centroid within cell $i$, respectively, in units of meters; and $Z(x_i, y_i)$ to refer to the simulated density, in units of number per 10 $m^2$, within cell $i$. See Appendix B for details of the simulation of populations.

## Survey simulations

The simulated surveys were based on quadrat sampling, which is common practice in ecological surveys. The geographic range of the simulated population was divided into a grid of 1 n.mi. × 1 n.mi. contiguous cells; this was our spatial sampling frame and each cell was a quadrat, the sampling unit. A sample of cells was selected and the population density within a cell was observed and multiplied by a sampling error term, $\varepsilon_i$. The density of fish "caught" in the $i$th sampled cell (number per 10 $m^2$) was designated as

$$z(x_i, y_i) = z_i = Z(x_i, y_i) \times \varepsilon_i$$

where $Z(x_i, y_i)$ is the simulated density of the population at that cell (see eq. B1 in Appendix B), and $\varepsilon_i$ is a random lognormal variate, representing small-scale variability about the densities within a cell. The variance for the lognormal error term was obtained from the variance within stations with multiple hauls in the historic database, that is, where many samples were taken at the same location on the same day.

For each of the 100 simulated populations, 100 simulated samples were generated using each of the six survey designs. Each survey was designed to have approximately the same sample size, $n$, to facilitate the comparisons of the designs. Mean larval density was estimated from each simulated sample, and the ability of the survey method to recover the parameters of the simulated population was examined by measuring bias and precision.

For every survey design except random, we grouped the grid of 8857 cells into 10 n.mi. × 10 n.mi. "blocks", so that each block contained 100 cells (Fig. 3). For the unequal probability sampling and the stratified systematic sampling, we calculated the mean densities within each block from all 100 simulated populations and used these to create probabilities for sampling within each block and for creating strata boundaries. Averaging densities over all 100 populations is comparable to using data from a time series of previous surveys to set sampling parameters for a future survey, as opposed to conducting a pilot survey to determine sampling parameters.

Graphic examples of each survey design are provided (Fig. 4). The formulas for the unbiased estimators of the mean ($\mu$) and variance ($\sigma$) are provided for each classic survey design in Appendix C, Table C1 and for the adaptive cluster survey design in Appendix D, Table D1. For the sake of broad applicability, all estimates include the finite population correction factor, $(N - n)/N$, even though this number is very close to unity because our value of $N$ is so large relative to $n$.

For systematic cluster, stratified systematic, and the adaptive cluster designs, we used conventional "cluster" sampling where each of the 100 cells within blocks is a single "primary unit" or cluster of cells. The cells within a primary unit are called "secondary units" and have the same position in each block. This follows Cochran's aligned or "square grid" systematic sample in two dimensions (Cochran 1977). A primary unit, or randomly chosen starting position, was sampled, then the corresponding secondary units were sampled per primary unit, in the same relative positions in each block.

### *Adaptive cluster sampling design*

In adaptive cluster sampling, if the density at a sampled unit satisfies a preset criterion, then further sampling occurs around that unit (Thompson 1991). We followed Thompson's terminology, except for his definition of cluster. (Note: Thompson's definition of a cluster is a group of adaptively sampled stations, as opposed to Cochran's definition of cluster, as defined above.) The initial sample was a systematic cluster sample, similar to what we used for the systematic cluster survey; these stations were occupied independently of what previous observations were made. The sampling pattern for the additional adaptive stations was that of a square grid about the initial station, with adaptive stations 5 n.mi. immediately northeast, southwest, northwest, and southeast of the initial unit that met the criterion. These additional four stations comprise the neighborhood of the initial station. If any of these stations met the criterion, additional stations were added using the same pattern and spacing (Fig. 5). We chose this spacing because it (*i*) was smaller than the observed patch size (mean patch size was 10 n.mi.$^2$), (*ii*) helped limit the sample size, and (*iii*) overlapped the initial grid, insuring adjacent neighborhoods had coincident stations. At this point, our adaptive procedure ends and the next station on the initial grid is sampled, unlike Thompson's procedure, where the adaptive sampling continues until no more stations meet the criterion. The set of overlapping neighborhoods all spawned by a single initial

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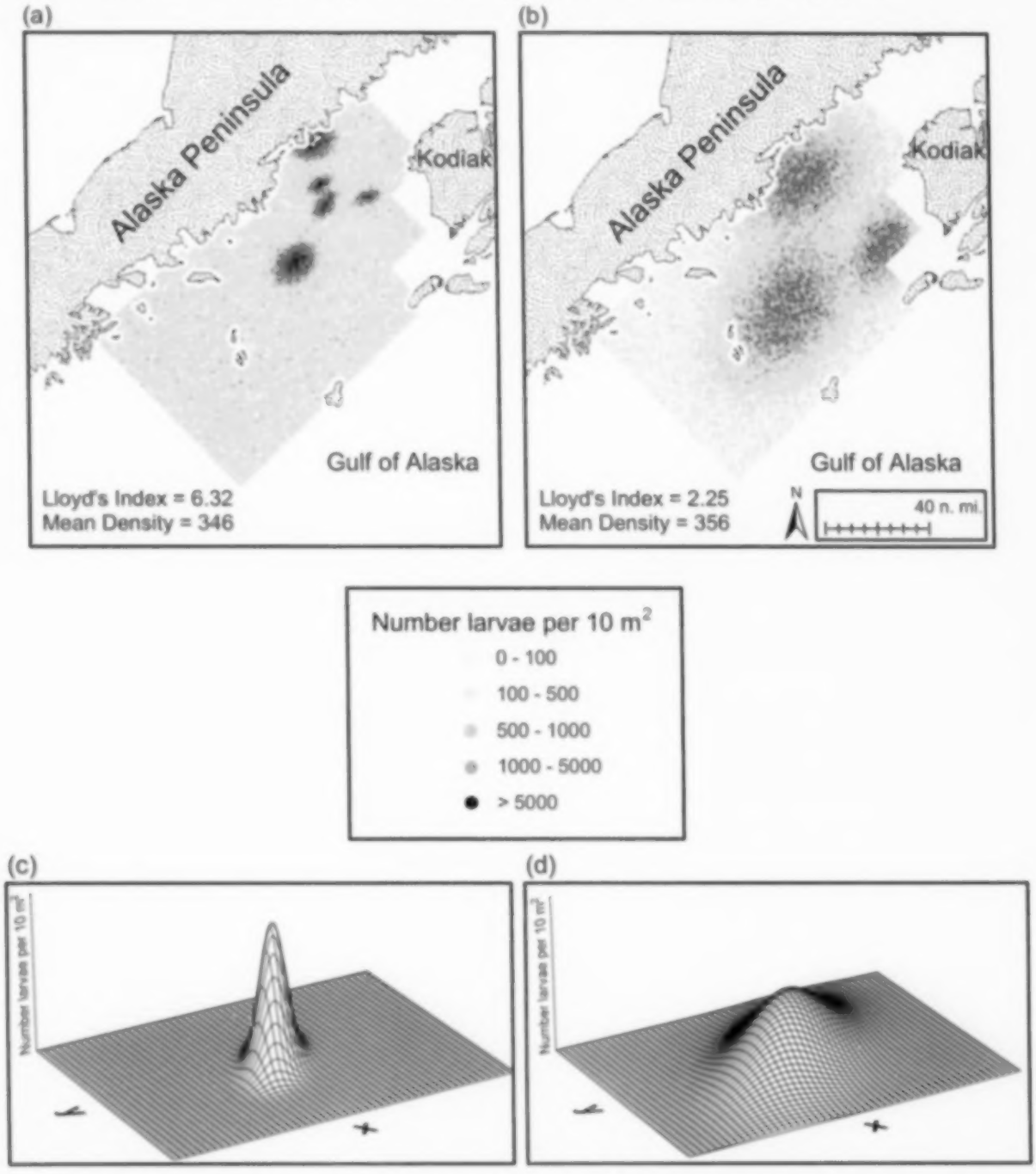
**Fig. 1.** Simulated populations of (*a*) high patchiness and (*b*) low patchiness. Single simulated patch of (*c*) high patchiness and (*d*) low patchiness based on bivariate normal probability distribution (see Appendix B for details of simulating a single patch).




station, excluding stations within the neighborhoods that do not meet the criterion, is called a network.

To control the sample size, we employed three methods: (*i*) restrict the number of iterations of testing for the criterion, (*ii*) use noncontiguous sampling units to form neighborhoods, and (*iii*) stop adaptive sampling and finish sampling the survey area with a systematic design in a second strata. In the first method, for each station in the initial sample, we allowed only two iterations of adding adaptive stations, that is, if an "A" station (initial sample) met the

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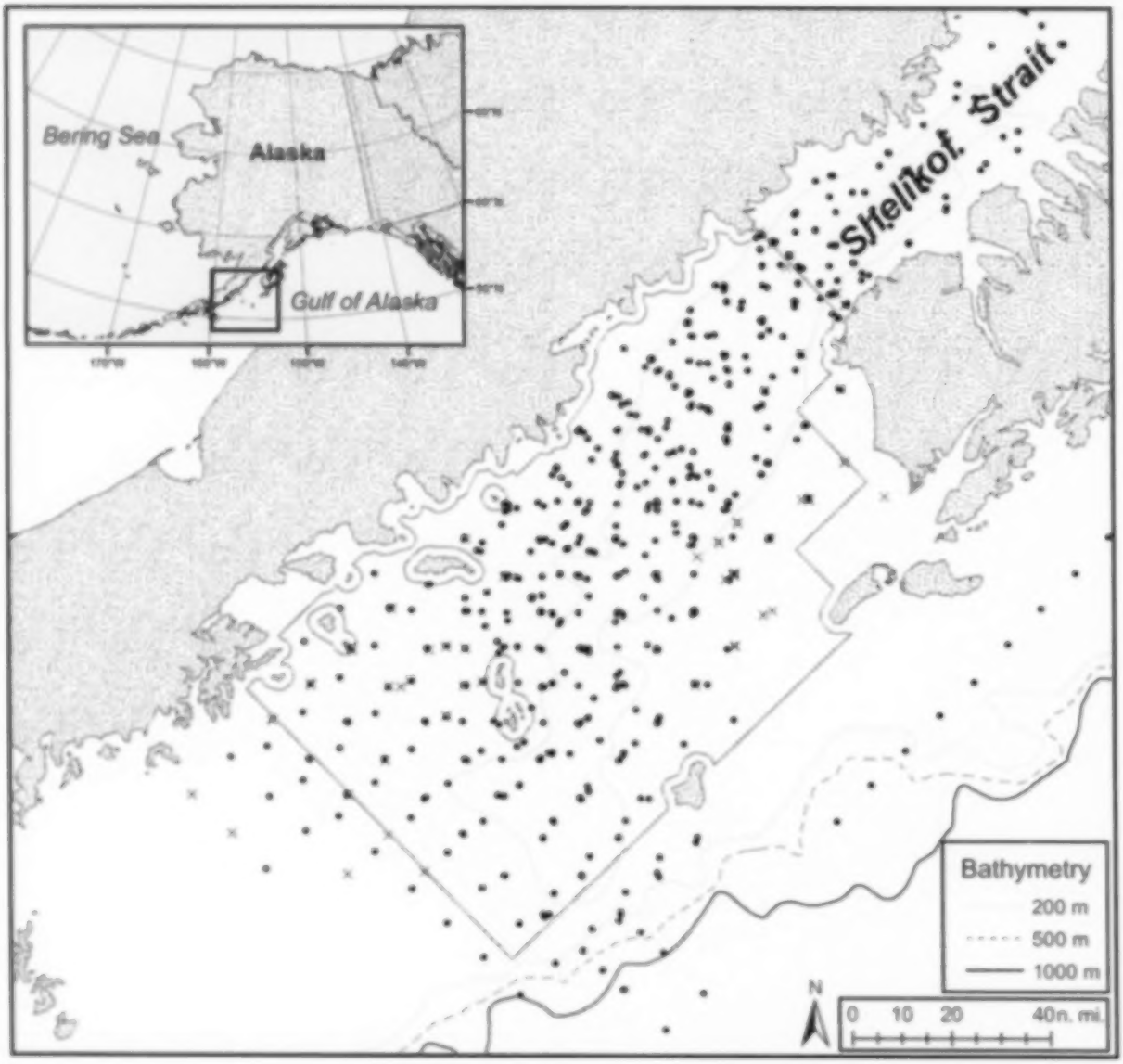
**Fig. 2.** Map of Shelikof Strait in Alaska, USA, showing stations with 0 catch (shown with × symbols) and stations with positive catches (shown with solid dots), with boundary of simulated population.




criterion, then the four stations in the neighborhood of A were sampled (called "B" stations). If any B station met the criterion, then the stations in the neighborhood of B stations were sampled (called "C" stations). Then we stopped the adaptive sampling and continued with the initial sampling plan. Quinn et al. (1999) called this a stopping rule with two iterations. This yielded possible sampling of 12 additional stations per A station (4 possible B stations plus 8 possible C stations). We called this a "district" (Fig. 5).

The second method we used to reduce sample size was to define the neighborhood to be noncontiguous grid cells. The spacing of the adaptive stations five cells apart allowed networks to grow beyond the extent of a single district, that is, C stations overlapped A stations, therefore allowing networks to overlap and become one large network (Fig. 5).

The third method for controlling sample size, that is dividing the survey area into two strata, was accomplished by not fixing the strata boundary before the survey; instead, we ceased adaptive sampling when the number of stations left to sample before reaching the desired sample size equaled the number of blocks yet to be sampled. This is a form of poststratification; therefore, the appropriate stratified estimator was used.

The criterion value used to initiate adaptive sampling was a density greater than the 85th percentile of the densities from the 100 simulated populations. This is equivalent to

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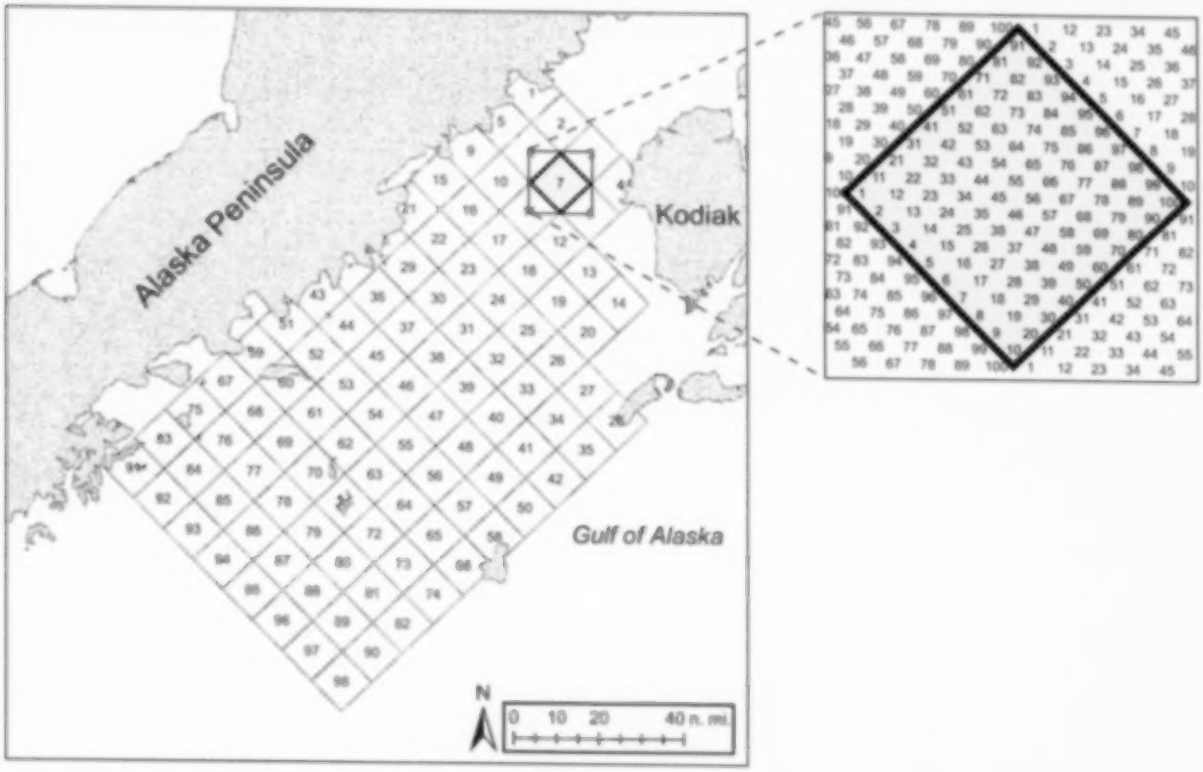
**Fig. 3.** Map showing the survey area gridded into 10 nautical mile (1 n.mi. = 1.852 km) × 10 n.mi. blocks, labeled 1–98, each of which is divided into 1 n.mi. × 1 n.mi. cells, labeled 1–100.




using order statistics as recommended by Thompson and Seber (1996). Basing the criterion on all 100 simulated populations is equivalent, in practice, to using past survey data, as opposed to conducting a pilot survey, to compute the criterion, similar to how we computed the sampling parameters for unequal probability sampling and stratified systematic sampling. We determined this percentile by calculating the proportion of A stations that we could allow to be adaptively sampled to meet the desired sample size.

The estimators commonly used for adaptive sampling are the Hansen–Hurwitz (HH) and the Horvitz–Thompson (HT) estimators. We considered three additional estimators, and all five are described in Appendix D. Each of the five adaptive estimators was applied to stratum 1 only. The final estimate for each sample was computed by combining the two strata estimates using the usual stratified estimators (see Appendix C, Table C1). The variance of stratum 2 was estimated using the estimator from systematic sampling, treated as random, because it had only one cluster.

### *Classic sampling designs*

Random sampling is sampling with equal probability, while unequal probability sampling assigns different selection probabilities to the individual sampling units. Sampling with probability proportional to a measure of size is a special type of unequal probability sampling (Jessen 1978). In our case, the probability was proportional to the mean density within each 10 n.mi. × 10 n.mi. block, averaged over all 100 simulated populations. This mean density was our measure of size.

The systematic survey design had only one primary unit (starting point) to demonstrate a very common survey design, because multiple starting points for systematic sampling are seldom used in practice. Traditionally, the AFSC ichthyoplankton surveys use a modified systematic sampling design. It is common in marine science to sample systematically along a grid rather than randomly to get even coverage of the survey area and to make the most efficient use of ship time. This is often done with a single random start, which theoretically would yield a "cluster" of one sample. Because no variance can be calculated from a sample of one cluster (Cochran 1977), a simple random sample estimator is used with this design, where each station is considered a sampling unit, with the assumption that there is no spatial periodicity in the data that coincides with the systematic spacing of the sample (Stehman and Overton 1994). Any deviation from this assumption will appear as bias in the estimates of the mean and variance. If one uses more than one random starting point, resulting in multiple clusters, then a variance can be calculated (Cochran 1977). We call this systematic cluster design, and we simulated this design using two random starting points.

Stratified systematic survey designs are obtained by dividing the elements of the sampling frame into groups, or strata, such that the variability within strata is believed to be less than the variability between strata. For simplicity, we

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**Fig. 4.** Maps showing examples of the spatial arrangement of six different survey designs: (*a*) adaptive cluster (adaptive stratum is dark gray, nonadaptive stratum is light gray, and dots of same shade represent clusters), (*b*) random, (*c*) unequal probability (intensity of shading indicates sampling probability within the block), (*d*) systematic using single cluster, (*e*) systematic cluster (dots of same shade represent clusters), (*f*) stratified systematic showing two strata (dots of same shade represent clusters; blocks of same shade indicate strata).

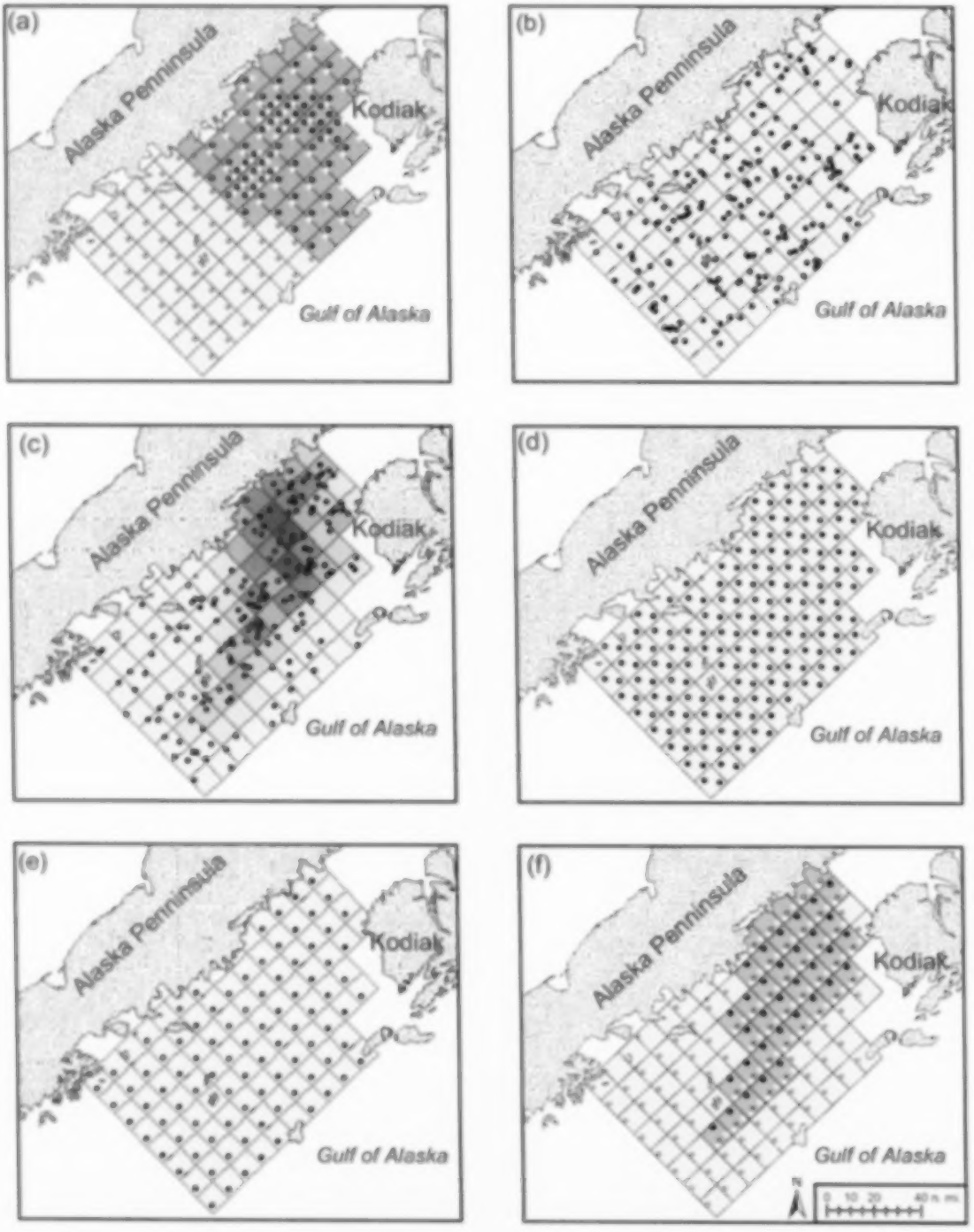


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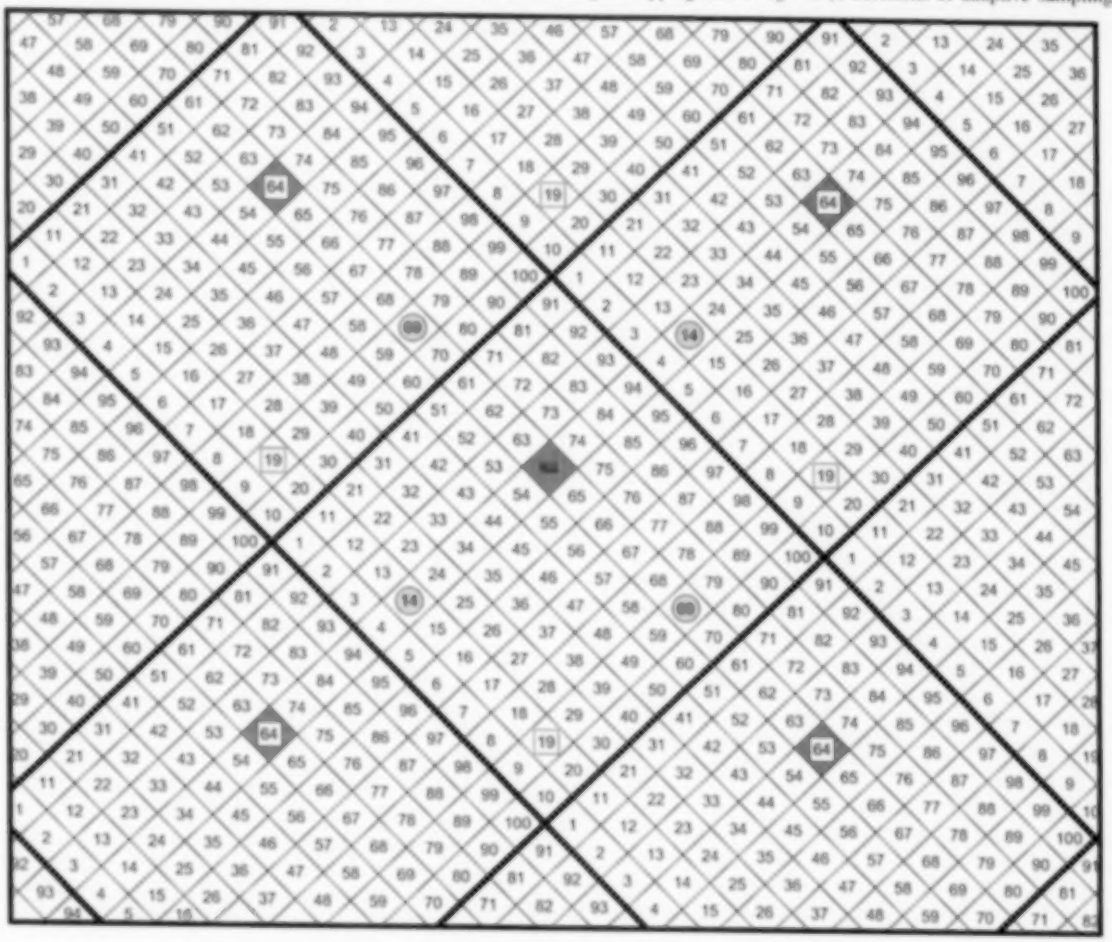
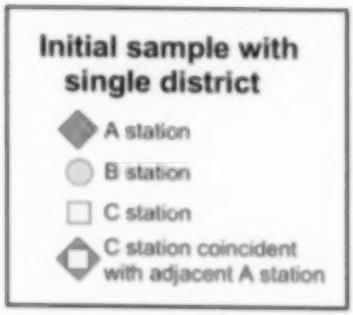
**Fig. 5.** Adaptive sampling design. Map shows a "neighborhood" (i.e., an *A* station with four surrounding *B* stations) and a "district" (i.e., 13 *A*, *B*, and *C* stations) for the adaptive survey. This is the result of using a stopping rule of $s_0 = 2$ (2 iterations of adaptive sampling).






chose to use just two strata. Appropriate strata boundaries were chosen using the mean densities within each 10 n.mi. × 10 n.mi. block, averaged over all 100 simulated populations. Blocks with means larger than the grand mean of all cells in all 100 populations were assigned to stratum 1 and the other blocks to stratum 2. Allocation of number of sampled cells to the strata was proportional to the standard deviation of the simulated densities within each stratum, averaged over the 100 simulated populations; thus, more stations were sampled in strata with higher average standard deviations.

### Survey design comparisons

In our simulation, we based our comparison of survey designs on the bias, precision, and MSE of the estimated mean

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**Table 2.** Formulas used to compare properties of estimators among different survey designs.

| | Mean | SE |
|---|---|---|
| True population | $\mu_l = \frac{\sum_{i=1}^{N} Z_l(x_i, y_i)}{N}$ | $\sigma_l = \sqrt{\mathrm{Var}(\hat{\mu}_l)} = \sqrt{\frac{\sum_{s=1}^{S}(\hat{\mu}_{sl} - \bar{\mu}_l)^2}{S}}$ where $\bar{\mu}_l = \frac{1}{S}\sum_{s=1}^{S}\hat{\mu}_{sl}$ |
| Relative bias | $\frac{1}{L}\sum_{l=1}^{L}\left[\frac{(\bar{\mu}_l - \mu_l)}{\mu_l}\right] \times 100$ | $\frac{1}{L}\sum_{l=1}^{L}\left[\frac{(\bar{\sigma}_l - \sigma_l)}{\mu_l}\right] \times 100$ where $\bar{\sigma}_l = \frac{1}{S}\sum_{s=1}^{S}\hat{\sigma}_{sl}$ |
| Relative imprecision | $\frac{1}{L}\sum_{l=1}^{L}\left[\frac{\sqrt{\mathrm{Var}(\hat{\mu}_l)}}{\mu_l}\right] \times 100$ where $\mathrm{Var}(\hat{\mu}_l) = \sigma_l$ | $\frac{1}{L}\sum_{l=1}^{L}\left[\frac{\sqrt{\mathrm{Var}(\hat{\sigma}_l)}}{\mu_l}\right] \times 100$ where $\mathrm{Var}(\hat{\sigma}_l) = \frac{\sum_{s=1}^{S}(\hat{\sigma}_{sl} - \bar{\sigma}_l)^2}{S}$ |
| Relative $\sqrt{\mathrm{MSE}}$ | $\frac{1}{L}\sum_{l=1}^{L}\left[\frac{\sqrt{\frac{1}{S}\sum_{s=1}^{S}(\hat{\mu}_{sl} - \mu_l)^2}}{\mu_l}\right] \times 100$ | $\frac{1}{L}\sum_{l=1}^{L}\left[\frac{\sqrt{\frac{1}{S}\sum_{s=1}^{S}(\hat{\sigma}_{sl} - \sigma_l)^2}}{\mu_l}\right] \times 100$ |

**Note:** $Z_l(x_i, y_i)$ = density at the $i$th cell of the $l$th population; $\hat{\mu}_{sl}$ and $\hat{\sigma}_{sl}$ are the estimated mean and SE of the mean from the $s$th sample of the $l$th population, respectively; $N$ = total number of cells; $L$ = total number of populations; $S$ = total number of samples per population; and MSE = mean squared error.

population density, $\hat{\mu}$, and its estimated SE, $\hat{\sigma}$, for each survey design. The MSE is often used to compare estimators having different amounts of bias and precision, that is

$$\begin{aligned}\mathrm{MSE} &= E(z_i - \mu)^2 = E[(z_i - \hat{\mu}) + (\hat{\mu} - \mu)]^2 \\ &= E(z_i - \hat{\mu})^2 + (\hat{\mu} - \mu)^2 \\ &= (\text{Variance of } z_i) + (\text{Bias})^2\end{aligned}$$

where $\mu$ is the true mean of the population, and $\hat{\mu}$ is the mean of the sampled values of $z_i$ (Cochran 1977). For ease of comparison, we put all these parameters in the same units as the population mean, that is, for precision we used SE instead of variance and we took the square root of the MSE. All measures of survey performance were expressed as a percentage of the population mean density (Table 2), thus making them relative. Results were reported for two separate groups, i.e., 50 populations with a high level of patchiness and 50 populations with a low level of patchiness. Note that the true mean population density, $\mu_l$, is the average value of all cell densities for the $l$th population; however, the "true" population SE for the $l$th population, $\sigma_l$, is actually an approximation, because it is the square root of the variance about the 100 sample means for the $l$th population rather than the variance about sample means from all possible samples. The relative bias, precision, and $\sqrt{\mathrm{MSE}}$ for a particular survey design were computed for each population and then averaged over the $L = 50$ populations within each population group (high patchiness and low patchiness).

Hypothesis testing was performed to detect if relative bias of the mean differed significantly between survey designs within each population group (high patchiness and low patchiness) by performing a one-way analysis of variance (ANOVA), where the dependent variable was the absolute value of the relative bias for each population, the single fixed factor was survey design, and populations were replicates. If the survey design factor was significant, then Fisher's LSD (least significant difference) multiple comparisons (Milliken and Johnson 1992) were performed to see which were different. This testing was done for all six performance measures, that is, the relative bias, SE, and $\sqrt{\mathrm{MSE}}$ for estimates of both the mean and SE for both the high- and low-patchy populations.

## Results

### Simulated populations

We simulated two sets of 50 populations: one set had a high level of patchiness and the other exhibited a low level of patchiness. Examples of simulated populations with high and low patchiness are provided (Fig. 1). The simulated populations had values of Lloyd's index of patchiness (Lloyd 1967; Pielou 1969) that ranged between 6.2 and 7.7 and between 2.0 and 2.2 for the high- and low-patchy populations,

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respectively. The range of Lloyd's index for our nine historical cruises was 1.6–3.3, with most of these falling within the range of the low-patchy simulated populations. We wanted to examine the performance of the survey designs on populations even more patchy than our historical cruises, so we used values for each of the individual population parameters, such as patch size and maximum patch density, that were at the extreme of the observed range of values from the historical cruises to simulate the more patchy populations. This resulted in populations with a higher Lloyd's index than the historical data because none of the observed cruises had extreme values for all of the population parameters, whereas the simulated high-patchy populations did. Thus, the results from sampling the low-patchy populations are relevant to populations with spatial distributions similar to larval walleye pollock, while the results from sampling the high-patchy populations apply to populations with more exaggerated patchiness.

After simulating the populations, we then sampled the populations to obtain estimates using both adaptive estimators and classical estimators. We first looked at the results of the adaptive cluster sampling, chose the best adaptive estimator, then compared this with the classical estimators to determine which was the best overall survey design.

### Comparison of adaptive cluster estimators

Detailed results of the comparison of the five adaptive cluster estimators are provided in Appendix D. We concluded that HH and HT perform equally well and better than the other three estimators considered. However, we recommend the HH estimator over HT because the HH estimator never produces a negative variance estimate and it is much easier computationally.

### Comparison of survey designs

We compared the six survey designs using the HH estimator for the adaptive cluster survey. In general, the estimators for high-patchy populations performed worse than the low-patchy populations, with the difference being most pronounced in the imprecision and $\sqrt{\text{MSE}}$ of both the mean and SE (Fig. 6).

Although the adaptive cluster estimator (HH) had the greatest bias of the mean compared with the other survey designs, it still underestimated the mean by less than 0.8% of the mean for high-patchy and 1.4% for low-patchy populations (Fig. 6). The biases of the other estimators were considered negligible according to Cochran (1977), because they fall below 10% of the SE. Comparing precision about the mean, the random estimator performed significantly worse than all others (Table 3) for high-patchy populations (at about 18%).

Looking at the $\sqrt{\text{MSE}}$ values of the mean, the differentiation amongst the estimators was greatest for the high-patchy populations, with random being significantly higher than all others and systematic and stratified systematic being significantly lower (Table 3). Within low-patchy populations, the $\sqrt{\text{MSE}}$ of the mean for the random estimator was again the largest, but not significantly higher than that of unequal probability. The $\sqrt{\text{MSE}}$ values of the systematic and systematic cluster means were significantly lower than those of all others (Table 3).

The bias in the SE was greatest for the systematic estimator at about 7.5% for high-patchy populations and 3.5% for low-patchy populations (Fig. 6). The bias about the SE for the adaptive cluster design was significantly lower than that of the systematic and systematic cluster but significantly higher than that of the rest of the estimators for the high- patchy populations (Table 3). For low-patchy populations, the adaptive cluster bias about the SE was not significantly different from the stratified systematic bias and was significantly lower than the systematic, but significantly higher than all others.

The systematic cluster and adaptive cluster estimates of the SE were significantly the least precise for both high- and the low-patchy populations (Fig. 6, Table 3). The $\sqrt{\text{MSE}}$ values of the SE indicated that the stratified systematic and unequal probability survey designs delivered the best estimators of SE for high-patchy population groups, and the unequal probability and random survey designs produced the best estimators of SE for the low-patchy populations.

Clearly, there is no obvious best design for both high and low-patchy populations. Based on the $\sqrt{\text{MSE}}$ of the mean, the random design was a very poor choice for all populations and the systematic, systematic cluster, and stratified systematic designs' performances were superior for all populations. Looking at the $\sqrt{\text{MSE}}$ of the SE, the two systematic designs produced the worst estimates of the SE for both population groups, while stratified systematic, unequal probability, and random all performed admirably. We conclude that the stratified systematic survey design was the best overall estimator, regardless of the level of patchiness. This conclusion is well supported by examining Fig. 6. Even though the hypothesis tests in Table 3 do not clearly show superior performance of the stratified systematic design for the low-patchy populations, it performs consistently better in terms of the $\sqrt{\text{MSE}}$ of the mean and SE.

Another important observation is that using a single cluster with a systematic design did not significantly decrease the performance, based on $\sqrt{\text{MSE}}$ of the mean, when compared with a systematic survey with two clusters (when they have the same sample size); in fact, the systematic was significantly better for the high-patchy populations. Only in the case of the $\sqrt{\text{MSE}}$ values of the SE for low-patchy populations did the systematic cluster perform significantly better than the systematic (Table 3). This observation contradicts what Christman (2000) found; her simulated systematic surveys had a much higher bias in the variance, perhaps because her populations contained fewer primary units, and the probability of missing a cluster was large.

A valid concern with using a single cluster is that the SE estimator will be biased, and indeed it was, but the precision of the SE was sufficiently better for the single cluster systematic design than for the two-cluster design so that these two effects balanced each other out. As the number of clusters increase in the systematic cluster design, we expect the recision of the SE to improve, but this benefit would be tempered by the reduced number of samples within each cluster, given the total sample size did not change.

## Discussion

Choosing the best survey design to sample a patchy distribution should be based on minimizing bias and maximizing precision of the estimates of both the mean and the SE, for a given cost, which we equated to sample size. Bias, or the

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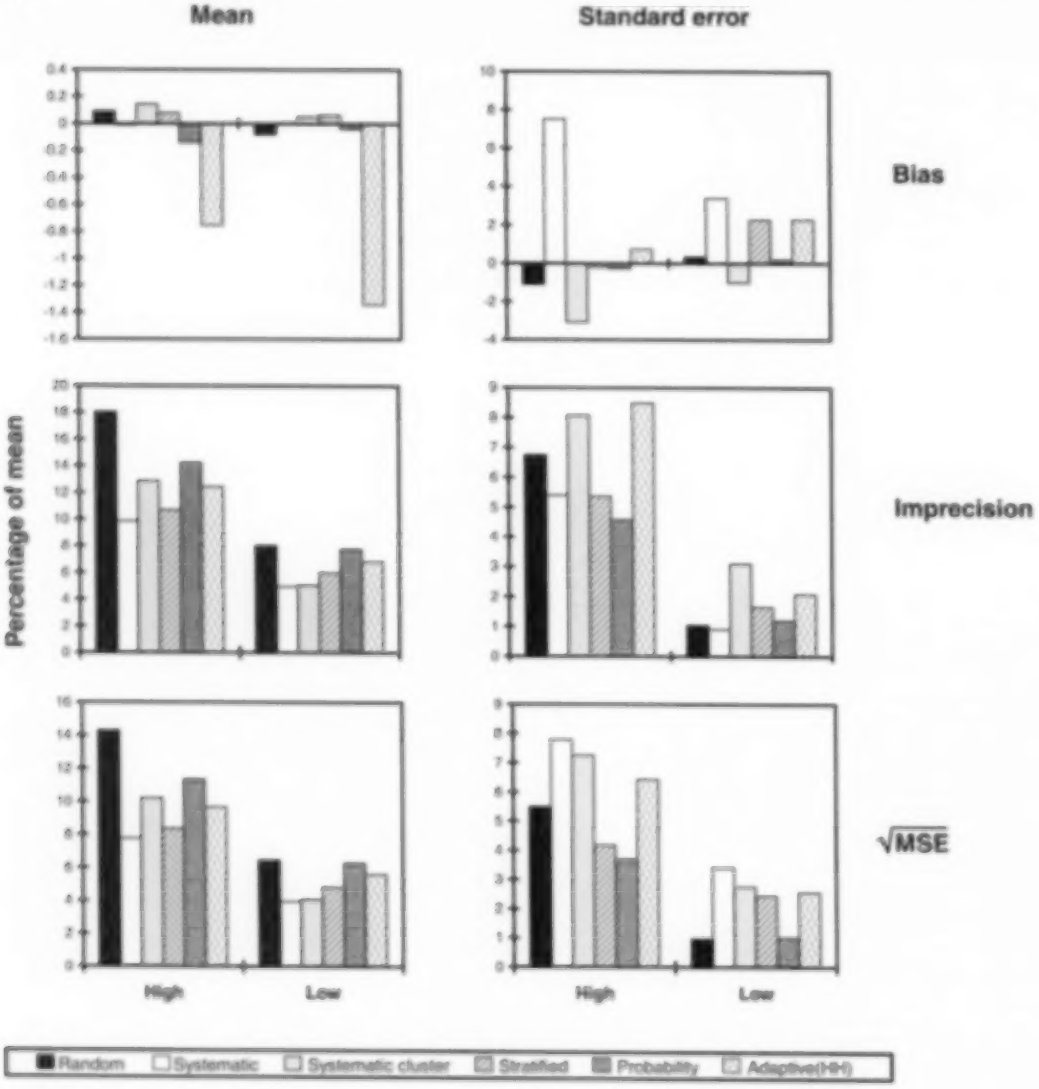
**Fig. 6.** The bias, imprecision, and $\sqrt{\text{MSE}}$ of the mean and SE averaged over the 50 high- and 50 low-patchy populations for the six survey designs.




difference between an estimate and the true value, is distinguished from precision, which is the differences among repeated measures (Sokal and Rohlf 1995). Precision is measured by the variance, that is, the smaller the variance, the more precise the estimator (we used SE instead of variance of the mean to keep all performance measures in the same units). The MSE is a measure of both precision and bias combined. Our results showed that the MSE of the mean of a patchily distributed population is determined more from precision (variance) than from bias.

The consequences of an inaccurate estimate of the mean are obvious, but the consequences of an inaccurate estimate of the SE are also important. If the estimated SE is inaccurate (i.e., overestimated or underestimated because of either bias or lack of precision or both), then the researcher will have less (if overestimated) or more (if underestimated) confidence in the estimate of the mean than warranted. This impacts the decisions based on the mean. If the mean is used in hypothesis testing, then the test will have incorrect power, resulting in incorrect test results. If the mean is used to set harvest rates (e.g., fishing quotas) and the SE is overestimated, then the resource manager may be cautious and set the quota lower than necessary. Conversely, if the SE is underestimated, then the resource manager may be less cautious and set the quota higher than the stock can support, potentially leading to overfishing.

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**Table 3.** Results of multiple comparison tests showing significant differences (at 5% significance level) among survey design estimators for both (*i*) high-patchy and (*ii*) low-patchy populations.

| | Adaptive (HH) | Unequal probability | Random | Stratified systematic | Systematic cluster | Systematic |
|---|---|---|---|---|---|---|
| **High-patchy** | | | | | | |
| Bias of mean | B | B | B | A | A | A |
| SE of mean | B | C | D | A | B | A |
| MSE of mean* | B | C | D | A | B | A |
| Bias of SE | B | A | A | A | C | D |
| SD of SE | D | A | C | B | D | B |
| MSE of SE* | C | A | B | A | D | D |
| **Low-patchy** | | | | | | |
| Bias of mean | D | C | B | A | A | A |
| SE of mean | C | D | D | B | A | A |
| MSE of mean* | C | D | D | B | A | A |
| Bias of SE | C | A | A | C | B | D |
| SD of SE | E | C | B | D | F | A |
| MSE of SE* | BC | A | A | B | C | D |

**Note:** The adaptive estimator is the Hansen–Hurwitz (HH) estimator. Estimators with the same letters indicate no significant difference.

*MSEs capture both bias and precision.

There are factors other than bias and precision that influence which survey design is used. One is the availability of prior information on the spatial distribution of a population. Of the six designs that we considered, three require prior information (stratified systematic, unequal probability, and adaptive cluster), and the other three do not (random, systematic, and systematic cluster). One might expect that designs that require prior information will perform better, but this is dependent on how well the prior knowledge applies to the present survey. Another factor that directly impacts the survey design choice is whether there is a single target species or whether many species are involved. If there is no single target species, there most likely will not be a single best design for all species, in which case designs that do not require prior information are the best compromise.

Our study shows that of the three applicable designs that require no prior knowledge (random, systematic, and systematic cluster), the random survey design was the least effective, that is, the $\sqrt{\text{MSE}}$ of the mean was the poorest of all the survey designs, although the $\sqrt{\text{MSE}}$ of the SE was moderate. Random sampling has inherent disadvantages as well, including (*i*) no way to deal with high variability in the data and its effect on the estimators other than increasing the sample size, (*ii*) difficult implemention in the field because of irregular spacing of sampled units, (*iii*) missed patches because of uneven spatial coverage, and (*iv*) data are poorly suited for spatial analysis, such as interpolation. Systematic sampling is much easier to implement and provides even coverage; however, multiple starting points (clusters) are seldom used in practice. Rather, each station sampled is considered to be a separate sampling unit, instead of part of a single cluster, and the sample is treated as if it were random (Schopka 1994; Wertheimer and Celewycz 1996; Edgar et al. 1997). From our simulation, we conclude that there was very little difference in bias, precision, and $\sqrt{\text{MSE}}$ between the use of a systematic design with a single cluster and using a systematic cluster with two clusters. Although the SE is slightly overestimated by the systematic design, this is mitigated by the improved precision of the SE. Therefore, our simulation shows that the convenience of sampling a single cluster does not seriously impact the bias and precision of the estimates.

Our interest in adaptive cluster sampling is primarily due to advantages reported in the literature. For example, adaptive cluster sampling (*i*) is reported to yield more precise estimates for patchy distributions (Brown 2003; Hanselman et al. 2003; Turk and Borkowski 2005), (*ii*) allows for increased observations of interest by concentrating additional sampling effort in those areas where there is higher density, and (*iii*) makes more efficient use of ship time by adding samples that are near the initial sample (Turk and Borkowski 2005).

The first two advantages mentioned above also apply to stratified systematic and unequal probability sampling. Unequal probability sampling is more precise if the selection probabilities are proportional to the values being observed and allows for concentration of sampling in areas of historically high fish densities. An example of unequal probability sampling in fisheries can be found in Dressel and Norcross (2005). Stratified systematic surveys yield more precise estimators if the strata create more homogeneous areas and may reduce the cost per observation by sampling more convenient groups. Stratified systematic sampling has the added advantage of providing separate estimates for each stratum without having to take another sample. However, if the strata are not appropriately chosen, the precision of the estimator may decrease. An example where a stratified systematic survey is used in fisheries can be found in Pennington et al. (2002).

In comparing adaptive cluster sampling with stratified systematic and unequal probability survey designs, the adaptive cluster survey is more stringent in that it requires absolute abundance information to determine the criterion that initiates adaptive sampling, and it requires information on

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the spatial distribution to specify the spacing of the added adaptive samples. Stratified systematic and unequal probability surveys only require relative abundance, which may be more constant from year-to-year than absolute abundance. For all three of these survey designs, we used the average absolute abundances and average spatial distributions, averaged over the 100 simulated populations. One possible reason that the adaptive cluster survey did not show marked improvement over the other designs is that the criterion that initiated adaptive sampling was the same for every population, that is, the 85th percentile of population densities from all 8857 cells, averaged over the 100 populations. This is equivalent in practice to using historical data to specify the criterion, as opposed to conducting a pilot survey. The consequence of this is that populations with a high mean abundance would exhaust the quota of adaptive samples early in the survey and leave much of the area to be systematically sampled, thus diluting the benefit of adaptive sampling. In practice, if we were to choose a percentile of a presurvey as the criterion for adaptively sampling, the adaptive estimator might perform better. However, the number of sampling units in the adaptive survey would have to be reduced by the number of units sampled in the presurvey, which would obviously worsen the adaptive estimator's performance.

One of the greatest weaknesses in adaptive sampling is the inability to control the sample size, and this is especially critical in marine surveys over large areas employing ships on a fixed project schedule and budget, which accrue large costs per sample. We modified Thompson's adaptive cluster design in three ways to limit sample size and allow for the greatest coverage: (1) we stopped adaptive sampling after two iterations, (2) we skipped four sampling units when adaptive stations were sampled, allowing networks to overlap, and (3) we divided the survey area into two strata and only adaptively sampled one stratum. Methods 1 and 3 introduce bias into the estimates, the more serious of which is method 1, the restriction of adaptive iterations. Using a stopping rule ($s_0 = 2$) is a significant deviation from Thompson's design, and as a result our networks were incomplete. However, the second method for controlling sample size, that is, spacing the adaptive stations five cells apart, helped to counteract this bias by allowing for overlapping districts. We think that our very small negative bias (less than 1%) for the HT estimator compared with Su and Quinn's (2003) positive bias of 6%–8% (with or without a stopping rule) and Cabral and Murta's (2004) extreme bias is due to our overlapping neighborhood structure that allowed the formation of large networks. This obviously produces smaller sample sizes than contiguous neighborhoods, but is only viable if the patch size is sufficiently large relative to the area spanned by the neighborhood. Our procedure of skipping over units is similar to adaptively sampling only cells midway between secondary units (Woodby 1998). Although Woodby applies this "neighborhood restriction" to a one-dimensional systematic adaptive cluster sample design, he mentions that it could be extended to two dimensions, as we did. A two-dimensional example where one unit is skipped in all four directions when sampling adaptively is given by Christman (1997).

By stopping the adaptive sampling when we reached a predetermined sample size limit minus the number of initial secondary units yet to be sampled, we successfully covered the entire survey area and kept the sample size approximately equal to that of the other survey designs. As a result, we poststratified our sample into an adaptively sampled strata and a nonadaptively sampled strata, which resulted in a biased estimate of the variance, but this bias decreases as the average sample size for each strata increases (Jessen 1978), and it had a negligible effect in our case.

Other approaches in the literature deal with these challenges in adaptive sampling, that is, choosing the criterion for initiation of adaptive sampling, and limiting sample size. In Hanselman et al. (2003), three different strategies for specifying the criterion were investigated. One strategy used the 80th percentile of historical data, which is similar to using the 85th percentile of all 100 simulated populations in this paper. This avoids the need for a presurvey and the introduction of bias by the criterion value being dependent on the sampling. However, using a percentile of historical data would only be useful for populations with low interannual variability.

In a simulation study, Su and Quinn (2003) used both order statistics and a stopping rule ($s_0 = 3$) to help limit the size of the sample. They conducted a presurvey and adaptively sampled the stations with highest density, where the number of these ($r$) was dictated by the time available for sampling. They found that the HH estimator had relatively high positive bias if the level of aggregation was high, the stopping rule ($s_0$) was small, and $r$ was large. The bias of the HT estimator was not affected much by the stopping rule unless $r$ was small, in which case the bias was reduced.

Lo et al. (1997) used a stratified, two-stage adaptive cluster design, which also restricted the number of adaptively sampled stations. Instead of a presurvey, an iterative method based on past cruises was used to determine the criterion value that would provide the right number of stations that time and resources would allow. However, this value proved to be too high and had to be changed during the survey, requiring the sample to be poststratified, as we did. Their results indicated that a simple stratified estimator, using all stations sampled in a restricted adaptive cluster survey design, was more precise than the stratified HT estimator.

Christman (2003) controls sample size with a Markov chain one-per-stratum design, i.e., a two-stage sampling design where the area is first divided into strata, a random-start systematic sample of one is taken, then wherever the sampled unit satisfies the specified criterion, a secondary systematic sample is taken within that stratum. For the designs that she describes, the HT estimator can only be evaluated when the criterion is $z_i > 0$ (rather than $z_i > c$, where $c$ is a value other than 0).

Brown (1996, 2003) states that to have an efficient adaptive survey, one must design the survey in such a way as to balance the network size (not too big) with the within-network variance (not too small), because the within-network variance generally decreases with network size. Brown's simulations found adaptive sampling to be most efficient with networks containing two to four units. She recommends using neighborhood definitions and the criterion value to limit the network size, as was done in this paper.

Another important consideration in sampling is cost. Several papers address this issue. Brown (1996) found that the

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average distance traveled for adaptive sampling was less than that for random sampling for all simulated populations, regardless of the degree of patchiness. Hanselman et al. (2003) measured travel time efficiency and found that adaptive sampling was more efficient than random sampling for sampling patchily distributed Pacific ocean perch (*Sebastes alutus*). We did not specifically compare distance traveled between our survey designs, but any survey design with a grid pattern (i.e., systematic, systematic cluster, stratified systematic, and adaptive cluster) has logistical advantages over unevenly spaced stations (i.e., random and unequal probability). Typically, time is required to process a sample after collection, and a grid pattern provides a consistent amount of time before collecting the next sample.

In conclusion, our simulation suggests that of the adaptive cluster estimators, HH and HT were the best overall, and because HH was easier to compute than HT and never yields a negative variance, the HH estimator is preferred. Christman (1997) also states that although her simulation study showed that the HT estimator was often more efficient, HH was less sensitive to changes in population. Nevertheless, our adaptive cluster survey design did not perform as well as the stratified systematic design and introduced many logistical problems compared with other designs. If prior information is available for a population, a stratified systematic survey design produces the best estimator. Without any information on the spatial distribution, a systematic survey design is best, and sampling a single cluster (using a simple random estimator) rather than multiple clusters does not appreciably impact the bias or precision of the estimated SE. These conclusions apply only to populations with spatial structure similar to the populations that we simulated, that is, populations that are widespread throughout the survey area with a few patches with a broad range of size and density and with considerable small-scale patchiness. However, both Christman (2000) and Cabral and Murta (2004) found that stratified designs out-performed adaptive sampling, and because there were fundamental differences in our simulated populations compared with theirs, these conclusions apparently apply to a broader range of clustered populations.

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## Appendix A. Definitions and notations

### Subscripts

$i$ = cell, 1 through $N$
$j$ = primary unit, 1 through $N_k$
$p$ = patch, 1 through $P$
$k$ = network, 1 through $\kappa$
$h$ = stratum, 1 through $H$
$l$ = simulated population, 1 through $L$
$s$ = simulated sample, 1 through $S$
$b$ = block, 1 through 98

### All survey designs

cell $i$ = 1 nautical mile (n.mi.) × 1 n.mi. of surface area (1 n.mi. = 1.852 km); the simulated population covers 8857 cells, $i$ = 1,2,…,8857

sampling unit = station = a sampling event at the center of each cell = column of water under the surface area of the bongo sampler frame, that is, a circle of 60 cm diameter or 0.283 $m^2$

$N$ = total number of cells = 8857

$L$ = number of populations = 100

$S$ = number of samples per population = 100

$(x_i, y_i)$ = location of the centroid of cell $i$; $x_i$ is the east–west position and $y_i$ is the north–south position

block = 10 n.mi. × 10 n.mi. square containing 100 of the 1 n.mi. × 1 n.mi. cells; there are 98 blocks in the population

$Z_i = Z(x_i, y_i)$ = simulated average number of larvae in a column of water under 10 $m^2$ of surface area, averaged over area of cell $i$; the simulated population consists of $N$ = 8857 population units

$\mu = \bar{Z}$ = population average = average number of larvae per 10 $m^2$ of surface area; this is the parameter to be estimated by each survey

$z_i = z(x_i, y_i)$ = simulated population unit, $Z_i$, multiplied by a sampling error term; this simulates the density of larvae, that is, number of larvae in the water column below a 10 $m^2$ of surface area, sampled somewhere within cell $i$

$\varepsilon_i$ = sampling error around mean density in cell $i$, which is a random lognormal variate

$P$ = number of patches in population

$\boldsymbol{\mu}_p = (\mu_{x,p}, \mu_{y,p})$ = location of the centroid of patch $p$

$\boldsymbol{\sigma}_p^2 = \begin{pmatrix} \sigma_{x,p}^2 & \rho_p \\ \rho_p & \sigma_{y,p}^2 \end{pmatrix}$ = parameters controlling the size and shape of patch $p$

$f_p(x_i, y_i | \boldsymbol{\mu}_p, \boldsymbol{\sigma}_p^2)$ = proportion of patch $p$ that occurs in cell $i$

$M_p$ = maximum density of larvae (number per 10 $m^2$) in patch $p$

$B(x_i, y_i)$ = number of larvae at location $(x_i, y_i)$ that are not part of any patch

$\eta$ = random lognormal variate multiplied to the simulated density for every cell to incorporate variability about the modeled densities

LI = Lloyd's index of patchiness

$n$ = number of cells sampled = number of stations in the sample

### Unequal probability sampling

$\pi_i$ = probability that cell $i$ is sampled

$\bar{z}_b$ = the mean density of larvae in block $b$, averaged over all 100 simulated populations

$\bar{z}_i'$ = $\bar{z}_b$ for every cell $i$ that is in block $b$, this assigning the same value to each cell within each block

### Systematic cluster sampling

primary unit = observations that are systematically selected based on the same starting point within each block, also called clusters in the literature. For

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systematic sampling, the simulated population is partitioned into 100 primary units.

$N_s$ = number of primary units in population

$n_s$ = number of primary units in sample

secondary unit = each cell within a primary unit. Each primary unit has on average 89 secondary units.

$M_j$ = number of secondary units in primary unit $j$

$\sum_{j=1}^{N_s} M_j$ = total number of secondary units in population (Thompson's MN) = 8857

$\bar{z}_j$ = average observed density of larvae in primary unit $j$

$z_{ij}$ = density at $i$th sampling unit in primary unit $j$

### Stratified sampling

$H$ = number of strata

$N_h$ = number of cells in stratum $h$

$N_s$ = number of primary units, same value for all strata

$n_h$ = number of primary units sampled in stratum $h$

$M_{hj}$ = number of secondary units in primary unit $j$ in stratum $h$

$z_{hij}$ = density at $i$th sampling unit in primary unit $j$ in stratum $h$

$\bar{z}_{hj}$ = average observed density of larvae in primary unit $j$ in stratum $h$

$\bar{z}_h$ = average observed density of larvae in stratum $h$

### Adaptive cluster sampling

(These definitions are generally consistent with those given in Thompson (1991), where he uses a systematic sampling design for the initial sample.)

criterion = rule for initiating adaptive sampling. We used the criterion that the observed density is greater than 85% of all densities in all 100 simulated populations.

initial sample = systematic sample with $n_s$ starting points.

neighborhood = the neighborhood of a sampling unit consists of itself and a group of stations around the initial sampling unit following a prespecified pattern. For our simulated adaptive survey, the neighborhood is a systematic grid of four units around the initial unit. The distance between the central unit and each of its four neighbors is 5 n.mi. (Fig. 5).

district = In this application of adaptive sampling, we restrict the number of iterations of testing for the criterion of interest and adding more neighborhoods to two. The district for a unit consists of the initial station, labeled *A*, and two possible levels of neighborhoods, labeled *B* and *C*. Specifically, the district for a secondary unit in the initial sample (an *A* unit) consists of itself, its neighborhood of four *B* units, and each *B* unit's neighborhood of three *C* units. (Note that there are only three *C* units in each *B* unit's neighborhood because the *A* unit is at the same location as one of *B*'s four neighbors.) We stop with the *C* units because each *C* unit's neighborhood includes an adjacent *A* unit that is already sampled (Fig. 5).

network = the subset of stations within a cluster (as defined by Thompson 1991) that satisfies the criterion.

$\kappa$ = number of networks

$z_k$ = the total density in the $k$th network

$n_k$ = the number of primary units that intersect the $k$th network (Thompson (1991) uses $x_k$)

$I_{jk}$ = 1 if the $j$th primary unit in the initial sample intersects the $k$th network and 0 otherwise

$I_k$ = 1 if the initial sample intersects the $k$th network and 0 otherwise

$\pi_k$ = probability that the initial sample intersects the $k$th network, that is, $P(I_k = 1)$

$\pi_{k_1,k_2}$ = probability that the initial sample intersects both networks $k_1$ and $k_2$

$s_0$ = stopping rule = number of iterations of adaptive sampling before stopping. This paper uses a stopping rule of $s_0 = 2$.

$N_s$, $n_s$, and $M_j$ have the same definitions as for systematic cluster sampling.

## Appendix B. Simulation of populations

### Estimating patch parameters

A patch was defined for our purposes as a region that has densities greater than one standard deviation (SD) above the grand mean over all densities (Fig. B1) (Stabeno et al. 1996). The large-scale spatial distribution (on the order of tens of nautical miles) of larvae was characterized by a few large patches close to the spawning area and lower densities of larvae distributed more homogeneously over the rest of the survey area. The small-scale distribution (on the order of metres) of larvae was characterized by a large, multiplicative variance due to small-scale patchiness.

Large-scale patchiness was defined by the number, location, size, and shape of the patches; maximum densities inside the patches; and densities outside of the patches. These characteristics were observed from the historical data and incorporated into the simulation model as parameters that each have a stochastic component.

The spatial patterns for all nine historical cruises were summarized individually by first interpolating densities over the survey area and then standardizing within years (subtracting the mean and dividing by the SD) so that each cruise had a mean of 0 and SD of 1. The interpolation method used was the inverse distance weighted method in the Spatial Analyst extension of ArcGIS (version 8.3, Environmental Systems Research Institute, 2002). The interpolated densities from each cruise were mapped, and the patches were identified and delineated. Irregularly shaped patches were conceptualized as two or more slightly overlapping elliptical patches (Fig. B1). The nine spatial distributions of standardized densities were then analyzed to determine values or probability distributions that best described each of the following parameters: (*i*) number of patches, (*ii*) location of the patches, and (*iii*) size and shape of the patches; the untransformed densities were used to determine (*iv*) maximum densities inside the patches and (*v*) densities outside of the patches. These parameters are defined as follows (all symbols are defined in Appendix A):

(*i*) The number of patches, $P$, was simulated by a random variable from a uniform probability distribution, ranging between three and six patches to be consistent with the observed number of patches in the historical data.

(*ii*) The location of each patch was simulated by selecting the location of the center of the patch. A center location

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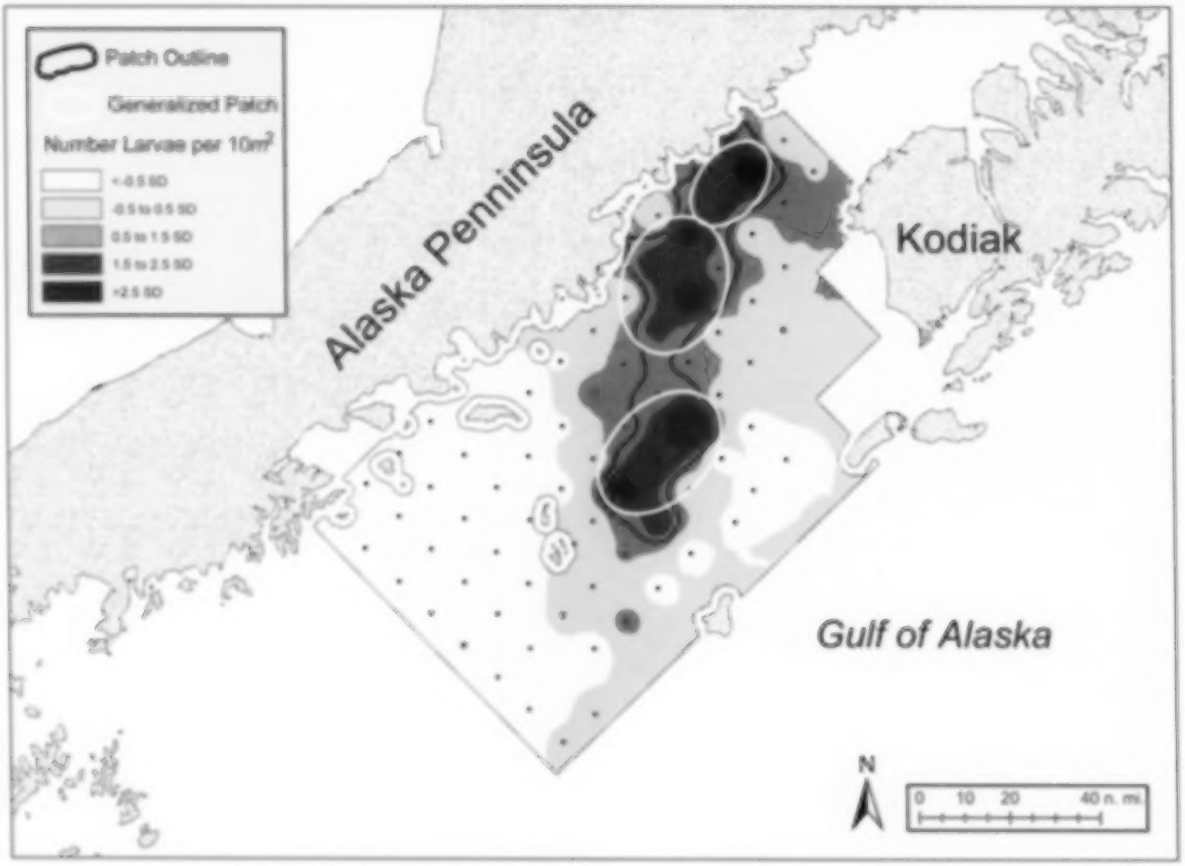
**Fig. B1.** Historical distribution of patch size and shape. Irregularly shaped patches were conceptualized as two or more slightly overlapping elliptical patches, outlined in white.




for each patch was randomly chosen with predetermined selection probabilities based on the total number of times that each cell was inside a patch in any of the cruises. Once a patch location was selected, subsequent patches within the population were located so that they did not substantially overlap the previous patches.

(*iii*) The size and shape of the $P$ patches were modeled by letting the portion of the $p$th patch (i.e., $f_p(x_i, y_i)$) that occurs at a location be proportional to the probability density of a bivariate normal probability distribution at $x_i$ and $y_i$, where the density has been rescaled so that the maximum density has the value of 1.0, that is

$$f_p(x_i, y_i | \boldsymbol{\mu}_p, \boldsymbol{\sigma}_p^2) = \exp\left\{\frac{-1}{2(1-\rho_p^2)} \times \left[\left(\frac{x_i - \mu_{x,p}}{\sigma_{x,p}}\right)^2 - 2\rho_p\left(\frac{x_i - \mu_{x,p}}{\sigma_{x,p}}\right) \times \left(\frac{y_i - \mu_{y,p}}{\sigma_{y,p}}\right) + \left(\frac{y_i - \mu_{y,p}}{\sigma_{y,p}}\right)^2\right]\right\}$$

where

$$\boldsymbol{\mu}_p = (\mu_{x,p}, \mu_{y,p})$$

and

$$\boldsymbol{\sigma}_p^2 = \begin{pmatrix} \sigma_{x,p}^2 & \rho_p \\ \rho_p & \sigma_{y,p}^2 \end{pmatrix}$$

This function was chosen because of its three-dimensional bell shape (Figs. 1*c*, 1*d*). Note that we used this function to describe the number of fish at each location, $x_i$ and $y_i$; we did not use it as a frequency distribution of the number of fish, which definitely does not have a Gaussian probability distribution. Instead, the $x_i$, $y_i$ locations were modeled with a bivariate normal distribution where the probability density at each location was proportional to the number of fish at the location. The bivariate mean of the bivariate normal density function, $\mu_{x,p}$ and $\mu_{y,p}$, is the location of the cell at the center of the $p$th patch, which was determined in the previous step. The other parameters of the function are SDs in the $x$ and y direction, $\sigma_{x,p}$ and $\sigma_{y,p}$, respectively, and correlation between $x$ and $y$, $\rho_p$. The values for $\sigma_{x,p}$, $\sigma_{y,p}$, and $\rho_p$ determined the size, shape, and orien-

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tation of the patch and were simulated to mimic the generalized patches (Fig. B1). The simulated values for $\sigma_{x,p}$ and $\sigma_{y,p}$ were small for the high-patchy populations and large for the low-patchy populations, with the constraint that all simulated values resulted in patch sizes that were within the range of the observed patch sizes in the historical data.

(*iv*) $M_p$ is the maximum density within the $p$th patch. The observed values of $M_p$ were correlated between patches within the historical cruises but varied widely between cruises. To replicate this, we simulated $M_p$ for every patch within a population using a lognormal random variable with the same mean, but allowed this mean to vary between populations. The high-patchy populations had simulated values of $M_p$ that were over an order of magnitude higher than the values for the low-patchy populations, again with the constraint that all simulated values were within the range of observed values in the historical data.

(*v*) Background numbers of fish, $B(x_i, y_i)$, at locations $x_i$ and $y_i$ that do not belong to any patch were simulated by a constant value for each population. The observed mean density outside of a patch in the historical data varied widely between cruises but was highly correlated with the mean of the maximum patch densities within the cruise ($r = 0.90$). The constant, $B$, was simulated for each population as a linear function of the mean of the maximum patch densities for that population.

### Simulating density at each location

The simulated density of fish, $Z(x_i, y_i)$, or number per 10 m$^2$ at each location $(x_i, y_i)$, was the sum of the densities at that location from all overlapping simulated patches, with the added background density level, that is

$$\text{(B1)} \quad Z(x_i, y_i) = \left[\sum_{p=1}^{P} f_p(x_i, y_i \mid \boldsymbol{\mu}_p, \boldsymbol{\sigma}_p^2) M_p + B(x_i, y_i)\right]\eta$$

where $P$ is the total number of patches, $f_p(x_i, y_i \mid \boldsymbol{\mu}_p, \boldsymbol{\sigma}_p^2)$ is the simulated relative density within the $p$th patch, $M_p$ is the maximum density within a patch, and $B(x_i, y_i)$ is the background density, all as defined above. A random lognormal variate, $\eta$, was then multiplied to the simulated density for every cell to incorporate variability about the modeled densities.

### Measuring high and low patchiness

Our populations were classified as high-patchy or low-patchy based on the values of the parameters used to simulate them. In an attempt to quantify the patchiness with a single metric, we computed Lloyd's index of patchiness (LI) (Lloyd 1967; Pielou 1969):

$$\text{LI} = 1 + \frac{\text{Var}(Z) - \bar{Z}}{\bar{Z}^2}$$

where

$$\bar{Z} = \frac{1}{8857}\sum_{i=1}^{8857} Z(x_i, y_i)$$

and

$$\text{Var}(Z) = \frac{1}{8857}\sum_{i=1}^{8857} [Z(x_i, y_i) - \bar{Z}]^2$$

Examples of simulated high- and low-patchy populations are shown in Figs. 1*a* and 1*b*.

## Appendix C

Appendix C appears on following page.

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**Table C1.** Equations used to calculate nonadaptive estimators of population mean and variance.

| Survey design | $\hat{\mu}$ | $\hat{\mathrm{Var}}(\hat{\mu})$ |
|---|---|---|
| Random | $=\sum_{i=1}^{n} z_i/n$ | $=\left(\frac{N-n}{N}\right)\frac{\sum_{i=1}^{n}(z_i-\hat{\mu})^2}{n(n-1)}$ |
| Unequal probability | $=\frac{1}{n}\sum_{i=1}^{n}\frac{z_i}{N\pi_i}$ where $\pi_i=\frac{z_i^*}{\sum_{i=1}^{N} z_i^*}$ | $=\left(\frac{N-n}{N}\right)\frac{\sum_{i=1}^{n}\left(\frac{z_i}{N\pi_i}-\hat{\mu}\right)^2}{n(n-1)}$ |
| Systematic cluster | $=\frac{1}{n_c}\sum_{j=1}^{n_c}\bar{z}_j$ where $\bar{z}_j=\frac{1}{M_j}\sum_{i=1}^{M_j} z_{ij}$ | $=\frac{N_c-n_c}{N_c}\sum_{j=1}^{n_c}\frac{(\bar{z}_j-\hat{\mu})^2}{n_c(n_c-1)}$ |
| Systematic | $=\sum_{i=1}^{n} z_i/n$ | $=\left(\frac{N-n}{N}\right)\frac{\sum_{i=1}^{n}(z_i-\hat{\mu})^2}{n(n-1)}$ |
| Stratified systematic | $=\frac{1}{N}\sum_{h=1}^{H} N_h\bar{z}_h$ where $\bar{z}_h=\frac{1}{n_h}\sum_{j=1}^{n_h}\bar{z}_{hj}$ and $\bar{z}_{hj}=\frac{1}{M_{hj}}\sum_{i=1}^{M_{hj}} z_{hij}$ | $=\frac{1}{N^2}\sum_{h=1}^{H} N_h^2\,\hat{\mathrm{Var}}(\bar{z}_h)$ where $\hat{\mathrm{Var}}(\bar{z}_h)=\frac{N_h-n_h}{N_h}\sum_{j=1}^{n_h}\frac{(\bar{z}_{hj}-\bar{z}_h)^2}{n_h(n_h-1)}$ |

**Note:** All symbols are defined in Appendix A.

## Appendix D. Estimators for adaptive cluster sampling

### Methods

The estimators commonly used for adaptive sampling are the Hansen–Hurwitz (HH) and the Horvitz–Thompson (HT) estimators. These estimators divide each observation by the draw-by-draw selection probability or the inclusion probability, respectively. Because these probabilities are not known for every unit in the sample, a modified HH estimator is often used, based on the number of times a unit in the initial sample intersects the $k$th network (all terms are defined in Appendix A). In contrast, a modified HT estimator is based on the partial inclusion probability, that is the probability that the initial sample intersects the $k$th network (Table D1) (Thompson and Seber 1996). One problem with the HT estimator is that the formula can yield a negative variance. Therefore, we also computed two other modifications of the HT variance estimator. The Yates–Grundy–Sen (YGS) estimator of the variance of the HT mean is usually nonnegative (Raj 1956; Thompson and Seber 1996), but is unbiased only for fixed sample sizes (Sarndal et al. 1992). Although our sample sizes were not fixed, they vary little because of our stopping rule and our stratification. Another estimator of the variance of the HT mean is the Brewer–Hanif (BH) estimator. It is conservative (slightly greater than the actual variance) and invariably nonnegative (Thompson 1992). The last estimators of the mean and variance that we considered were the Hajek–Sarndal (HS) estimators. Hajek's estimation of the mean is recommended when $\pi_k$ is not proportional to $z_k$. Sarndal et al. (1992) derived the equation for the variance of this estimator (Table D1).

### Results

In looking at the bias of the mean of the three adaptive cluster estimators of the mean, the HS estimator has a positive bias of about 12% and 8% for high- and low-patchy populations, respectively, whereas HH and HT have a negative bias of less than 2% (Fig. D1). The bias in the HS estimator was probably due to our particular survey design, because the sum of the reciprocal of probabilities of selection consistently underestimated $N$. The HS estimator had considerably more bias than HH and HT, was slightly more imprecise, and was no better in terms of estimating the SE; hence, the HS estimator was dropped from all further consideration.

The bias of the mean in the HH and HT estimators was only slightly greater than Cochran's (1977) rule of thumb for negligible bias, which is one-tenth of the SE. In terms of precision of the mean, both estimators performed worse for

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**Table D1.** Equations used to calculate adaptive cluster estimators of population mean and variance.

| Estimator* | $\hat{\mu}$ | $\hat{\mathrm{Var}}(\hat{\mu})$ |
|---|---|---|
| HH | $= \frac{1}{n_c}\sum_{j=1}^{n_c}\frac{1}{M_j}\sum_{k=1}^{n}\left(\frac{z_k I_{jk}}{n_k}\right)$ | $= \left(\frac{N_c - n_c}{N_c}\right)\frac{1}{n_c(n_c-1)}\sum_{j=1}^{n_c}\left[\left(\frac{1}{M_j}\sum_{k=1}^{n}\frac{z_k I_{jk}}{n_k}\right) - \hat{\mu}\right]^2$ |
| HT | $= \frac{1}{\left(\sum_{j=1}^{N_c} M_j\right)}\sum_{k=1}^{\kappa}\frac{z_k I_k}{\pi_k}$ | $= \left(\frac{N_c - n_c}{N_c}\right)\frac{1}{\left(\sum_{j=1}^{N_c} M_j\right)^2}\sum_{k_1=1}^{\kappa}\sum_{k_2=1}^{\kappa}\left(\frac{z_{k_1} z_{k_2} I_{k_1} I_{k_2}}{\pi_{k_1 k_2}}\right)\left(\frac{\pi_{k_1 k_2}}{\pi_{k_1}\pi_{k_2}} - 1\right)$ |
| | where $\pi_k = 1 - \binom{N_c - n_0}{n_c} \Big/ \binom{N_c}{n_c}$ and $I_k$ is as defined above except it is independent of the primary unit | where $\pi_{k_1 k_2} \neq 0$ is given by $\pi_{k_1 k_2} = 1 - \left[\binom{N_c - n_{0_1}}{n_c} + \binom{N_c - n_{0_2}}{n_c} - \binom{N_c - n_{0_1} - n_{0_2} + n_{0_1 k_2}}{n_c}\right] \Big/ \binom{N_c}{n_c}$ |
| YGS | Same as for HT | $= \left(\frac{N_c - n_c}{N_c}\right)\frac{-1}{2\left(\sum_{j=1}^{N_c} M_j\right)^2}\sum_{k_1=1}^{\kappa}\sum_{k_2=1}^{\kappa}\left(1 - \frac{\pi_{k_1}\pi_{k_2}}{\pi_{k_1 k_2}}\right)\left(\frac{z_{k_1}}{\pi_{k_1}} - \frac{z_{k_2}}{\pi_{k_2}}\right)^2$ |
| BH | Same as for HT | $= \left(\frac{N_c - n_c}{N_c}\right)\frac{1}{\left(\sum_{j=1}^{N_c} M_j\right)^2}\frac{\sum_{k=1}^{\kappa}\left[\frac{\kappa z_k}{\pi_k} - \left(\sum_{j=1}^{N_c} M_j\right)\hat{\mu}\right]^2}{\kappa(\kappa-1)}$ |
| HS | $\mu_{HT} = \sum_{k=1}^{\kappa}\frac{z_k I_k}{\pi_k} \Big/ \sum_{k=1}^{\kappa}\frac{1}{\pi_k}$ | $= \left(\frac{N_c - n_c}{N_c}\right)\frac{1}{\left(\sum_{j=1}^{N_c} M_j\right)^2}\sum_{k_1=1}^{\kappa}\sum_{k_2=1}^{\kappa}\left(\frac{\pi_{k_1 k_2} - \pi_{k_1}\pi_{k_2}}{\pi_{k_1}\pi_{k_2}\pi_{k_1 k_2}}\right)(z_{k_1} - \mu_{HT})(z_{k_2} - \mu_{HT})$ |

**Note:** All symbols are defined in Appendix A.
*HH, Hansen–Hurwitz; HT, Horvitz–Thompson; YGS, Yates–Grundy–Sen; BH, Brewer–Hanif; HS, Hajek–Sarndal.

high-patchy populations compared with low-patchy populations (12% and 7%, respectively) (Fig. D1). The ANOVAs and multiple comparison tests failed to detect significant differences between these two estimators in terms of bias, precision, or $\sqrt{\text{MSE}}$ about the mean for either the high- or low-patchy populations (Table D2).

The HH and the HT estimators of the SE were similar to each other, overestimating the SE by a negligible amount (Fig. D1). YGS and BH were by far the poorest estimators of the SE in terms of bias, overestimating by around 9% for high-patchy and 6% for low-patchy populations (Fig. D1). Although YGS and BH were the poorest estimators in terms of bias and $\sqrt{\text{MSE}}$ of the SE, BH was the most precise. However, because $\sqrt{\text{MSE}}$ captures both bias and precision, this was used as the final criterion for dismissing YGS and BH as desirable estimators for these data sets.

Two variance estimators (YGS and HT) produced negative estimates of variance, which are obviously invalid, although computationally possible. The frequency of negative variances for the HT estimator was higher overall for the high-patchy populations (6% for the high and 1% for the low). The incidence of negative variances for the YGS estimator was similar (7% for the high and 1.5% for the low). The occurrence of negative variances for HT has been observed by others (Rao and Singh 1973), but YGS has been reported to be usually positive (Thompson and Seber 1996). All negative variances were excluded for purposes of computing measures of bias and precision of the SE for these two estimators.

Of the two remaining variance estimators (having eliminated the HS, YGS, and BH estimators), there were no significant differences between the HT and the HH variance estimators for relative bias, SD, or $\sqrt{\text{MSE}}$ of the SE for high-patchy populations. For low-patchy populations, the HT is significantly smaller in terms of relative bias of the SE (Table D2). However, in terms of the relative $\sqrt{\text{MSE}}$ for both population groups for both mean and SE, there were no sig-

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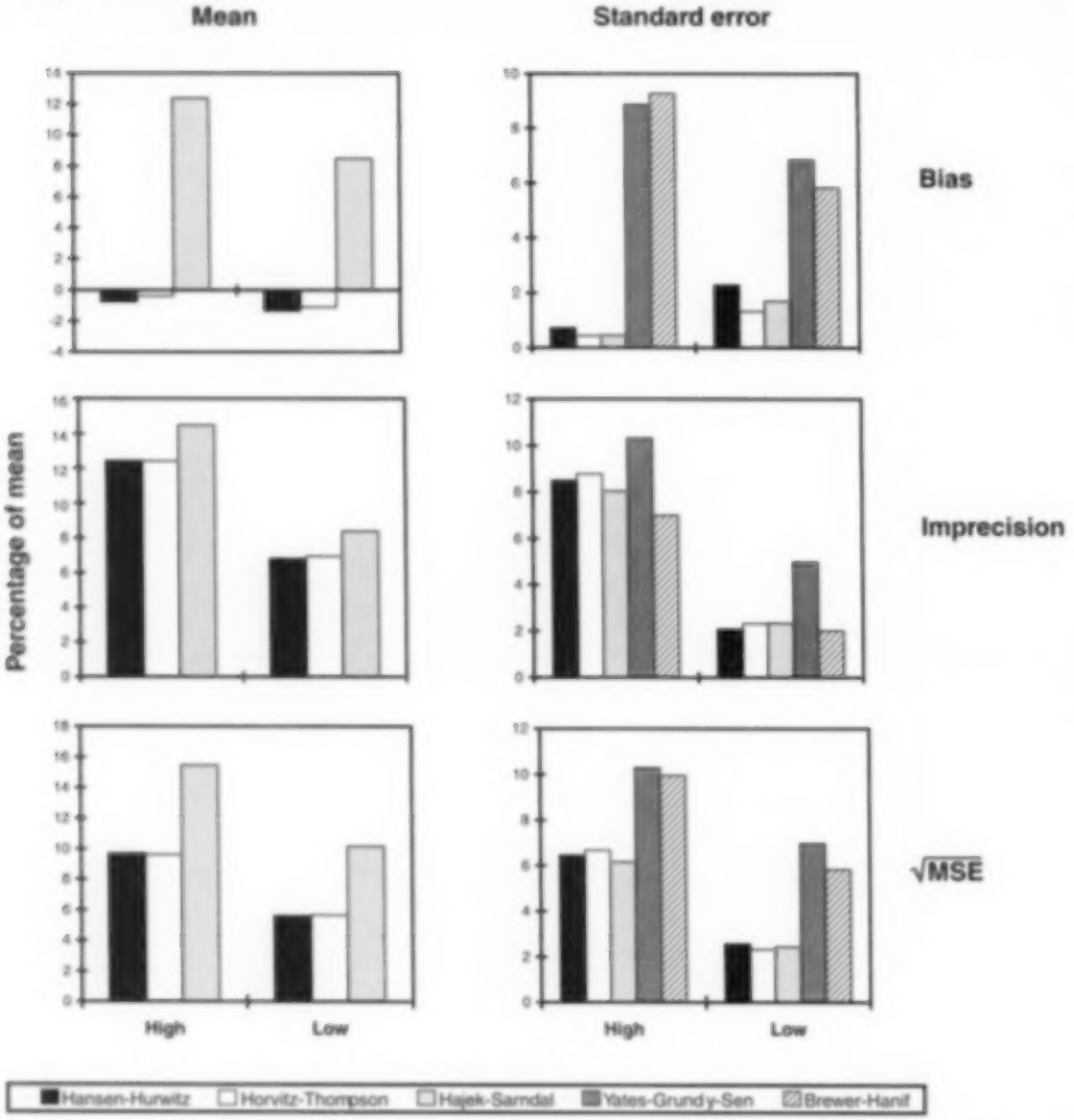
**Fig. D1.** The bias, imprecision, and $\sqrt{\text{MSE}}$ of the mean and SE averaged over the 50 high- and 50 low-patchy populations for the five different adaptive cluster estimators.




nificant differences (Table D2). Because this is a measure of both bias and precision combined and because the HH estimator has some advantages over the HT estimator (i.e., it never produces a negative variance estimate and it is much easier computationally), we recommend the HH estimator in practice.

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**Table D2.** Results of multiple comparison tests showing significant differences (at 5% significance level) among adaptive cluster survey design estimators for both (*i*) high-patchy and (*ii*) low-patchy populations.

| | Adaptive HH | Adaptive HT | Adaptive YGS** | Adaptive BH** | Adaptive HS |
|---|---|---|---|---|---|
| **High-patchy** | | | | | |
| Bias of mean | A | A | A | A | B |
| SE of mean | A | A | A | A | B |
| MSE of mean* | A | A | A | A | B |
| Bias of SE | A | A | B | B | A |
| SD of SE | B | B | C | A | AB |
| MSE of SE* | A | A | B | B | A |
| **Low-patchy** | | | | | |
| Bias of mean | A | A | A | A | B |
| SE of mean | A | A | A | A | B |
| MSE of mean* | A | A | A | A | B |
| Bias of SE | B | A | D | C | A |
| SD of SE | AB | B | C | A | B |
| MSE of SE* | A | A | C | B | A |

**Note:** HH, Hansen–Hurwitz; HT, Horvitz–Thompson; YGS, Yates–Grundy–Sen; Brewer–Haniff; and HS, Hajek–Sarndal. Estimators with same letters indicate no significant difference.

*MSEs capture both the bias and precision.

**The adaptive estimators BH and YGS are different estimators of the variance for the HT estimator of the mean. Therefore, the bias, SE, and MSE of the mean are the same as the HT estimator.

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# Life history variation parallels phylogeographical patterns in North American walleye (*Sander vitreus*) populations

**Yingming Zhao, Brian J. Shuter, and Donald A. Jackson**

**Abstract:** Walleye (*Sander vitreus*) is a native fish species in North America, and its zoogeographic range covers several climatic zones. Using multivariate statistical approaches and published growth data, we explored the association between climatic conditions (frost frequency, precipitation, air temperature, solar radiation, and cloud cover) and growth of walleye from 89 populations in North America. We found significant concordance between climatic conditions and walleye growth; however, the pattern of concordance differed among populations that originated from geographical regions that were colonized from different glacial refugia. This suggests that contemporary differences in walleye growth patterns related to local climatic conditions may have been shaped by evolutionary divergence that occurred among refugia during the last glaciation. We suggest that caution should be taken when assessing possible effects of climate variation and climate change on the life history traits of different walleye and other fish populations, especially when such assessments potentially include several genetically distinct groups. Procrustes analysis was shown to be an effective tool for characterizing how a multivariate set of response variables change in response to generalized changes in a multivariate set of independent variables.

**Résumé :** Le doré (*Sander vitreus*) est un poisson indigène d'Amérique du Nord dont la répartition géographique couvre plusieurs zones climatiques. Des méthodologies statistiques multidimensionnelles et des données de croissance tirées de la littérature nous ont servi à explorer l'association entre les conditions climatiques (fréquence des gels, précipitations, température de l'air, radiation solaire et nébulosité) et la croissance des dorés de 89 populations nord-américaines. Il existe une concordance significative entre les conditions climatiques et la croissance des dorés; cependant, les patrons de concordance diffèrent entre les populations qui proviennent de régions géographiques colonisées à partir de refuges glaciaires différents. Cela laisse croire que les différences actuelles dans les patrons de croissance des dorés reliées aux conditions climatiques locales ont pu être façonnées par la divergence évolutive qui s'est développée entre les refuges durant la dernière glaciation. Nous croyons qu'il faut être prudent lorsqu'on évalue les effets possibles de la variation climatique et du changement climatique sur les caractéristiques démographiques des différentes populations de dorés ou d'autres poissons, particulièrement si de telles évaluations incluent potentiellement plusieurs groupes qui sont génétiquement distincts. L'analyse Procuste s'est avérée être un outil efficace pour caractériser la manière dont un ensemble multidimensionnel de variables de réponse change en réaction à des changements généralisés dans un ensemble multidimensionnel de variables indépendantes.

[Traduit par la Rédaction]

## Introduction

Fish growth can be viewed as an integration of several physiological processes involving food consumption, metabolism, and other activities (Pitcher and Hart 1983). All these processes are influenced by environmental factors, such as temperature and food availability. Therefore, studies of fish growth require an explicit consideration of the environmental variables that characterize the ecosystem where the fish lives. Climatic conditions are a major component of these environmental variables.

Walleye (*Sander vitreus*) is a cool-water species (Hokanson 1977) and one of the most economically important fish species in the north-temperate fresh waters of North America. The optimal temperature range for walleye growth is 18–22 °C (Christie and Regier 1988). Because walleye

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**Fig. 1.** A map of 89 walleye (*Sander vitreus*) populations collected in this study; the native distribution (shaded area) of walleye populations in North America (redrawn from Colby et al. 1979) and five genetically distinct groups (polygons enclosed by thick lines — redrawn from Billington 1996). AT, Atlantic refugium; MS, Missouri refugium; MP, Mississippi refugium; HB, hybrids from MS and MP; MB, Mobile Basin drainage.

change their retinal response from positive phototaxis to negative phototaxis during their first year of life, adult walleye prefer feeding in a low-light environment (Ryder 1977). Therefore, both light and thermal conditions are expected to shape the growth pattern of walleye.

The native distribution of walleye in North America extends northward to the mouth of the Mackenzie River at the Arctic coast and southward to the Gulf Coast in Alabama (Fig. 1). Its eastern and western boundaries are marked by the Rocky Mountains and Appalachian Mountains, respectively (Regier et al. 1969). Owing to its economic importance as a primary sport and commercial fish species, the walleye has been widely introduced outside of its native range, particularly in western reservoirs (Goodson 1966), along the Atlantic seaboard, and elsewhere in North America (Whitworth et al. 1968; Munger 2002). Therefore, the present zoogeographic distribution of walleye is very broad and covers several climatic zones. There is wide variation in growth over this range, and significant associations between growth differences and climatic differences (i.e., air temperature) have been discovered (Colby et al. 1979; Colby and Nepszy 1981).

Colby and Nepszy (1981) found that variation in growing degree-days above 5 °C (GDD5) explained 72% of the variation in body length of first-year walleye in 78 populations with GDD5 ranging from around 1000 to 6000. Walleye populations with higher GDD5 values have a shorter life span, but tend to mature at younger ages. Beverton (1987) explained this phenomenon as a reproductive strategy for walleye to stabilize the value of lifetime egg production per female recruit over different climatic conditions and concluded that walleye is a species whose reproductive strategy is well adapted to climatic conditions in North America.

Using mitochondrial DNA markers, Billington et al. (1992) found that the three major haplotypes, dominant in walleye populations in North America, showed distinct geographic distributions, which reflected the postglacial recolonization of North America by walleye from three dif-

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ferent refugia: the Missouri refugium (MS), the Mississippi refugium (MP), and the Atlantic refugium (AT) (Fig. 1). After analyzing additional samples, especially for populations in the Mobile Basin (MB) drainage, Billington and Strange (1995) and Billington (1996) provided evidence for the existence of five genetically and geographically distinct groups of walleye populations in North America. In addition to the three groups from the refugia described above, a fourth walleye group (located in the southeastern states of Tennessee and Kentucky) was identified as a mixture of stocked fish from the AT and MP refugia (HB in Fig. 1). Gulf Coast walleye were found to be genetically distinct from other groups and were classified as a fifth group, the MB drainage group (Fig. 1) (Billington 1996). The inclusion of walleye populations into western Ontario and Minnesota in the MS refugium (Billington 1996) is debatable, however, because few populations (about three in the southern part of western Ontario) from western Ontario were characterized genetically and because both haplotypes 4 and 10 (the genotypes of populations from the MP and MS refugia, respectively) appeared in the Minnesota populations that were characterized (Billington et al. 1992). Genetic distinguishability among the groups implies that the walleye from different origins (i.e., different glacial refugia) experienced evolutionary divergence during the period of their geographic isolation from each other (Billington et al. 1992).

To summarize, walleye populations in North America can be separated into two large groups based on their recent history: one composed of all populations in the native range of the species and the other composed of introduced populations, located outside the native range. The populations in the native range can be further subdivided into five genetically distinct groups. However, no study has been done to test if there are differences among these groups in the response of their life history traits (e.g., growth) to variation in climatic conditions. In addition, the previous studies characterizing the variations in walleye life history traits (e.g., growth, fecundity, and maturation) over a large segment of its zoogeographic range have focused mainly on the effect of air temperature (Colby and Nepszy 1981; Baccante and Colby 1996). However, other climatic variables such as solar radiation and cloud cover should affect optical habitat of walleye and may lead to differences in walleye growth pattern.

In this study, we use published size-at-age data for walleye in North America to (*i*) assess the association between somatic growth and climatic conditions; (*ii*) explore spatial patterns in the concordance between somatic growth and climatic conditions; and (*iii*) investigate whether such concordance patterns between life history traits and environmental factors reflect the genetic divergence associated with ancestral linkage to different glacial refugia.

## Materials and methods

### Data collection

Data on walleye length-at-age were derived from two syntheses (Colby et al. 1979; Carlander 1997) of growth information for walleye in North America and from Stephenson and Momot (1991). The prior two syntheses were obtained by compiling data from more than 300 studies published in the scientific literature over the period from 1933 to 1993. A total of 89 walleye populations were included in the final growth database, with over 80% of these data collected over the period 1950–1990. These populations covered a latitudinal range from about 33°N to 59°N and a longitudinal range from about 75°W to 121°W (Fig. 1, Appendix A) and included both native and introduced populations. For the native group, we were unable to obtain data for populations located in the MB refugium region. Most length-at-age data were estimated from scales using back-calculation methods. Data from both sexes were combined to give overall average size-at-age values. The longest series of length-at-age data collected for the analysis was from ages 1 to 14, and the shortest series was from ages 1 to 5. Sexual dimorphism of older fish was evident for many walleye populations, and such differences in the growth rates between male and female walleye were population-specific and increased with age (Craig 2000; Munger 2002). The accuracy of scale ages also tends to decline with older fish. Therefore, we chose to work only on the first 5 years growth to minimize estimation problems associated with missing data, sexual dimorphism, and aging errors. Because size at older age is not independent of size at younger age (i.e., size at age ($i$) = size at ($i$ – 1) + growth increment over $i$th year of life, where $i$ = 1, 2, 3, 4, and 5), we only used age-specific estimates of annual incremental growth in our analyses. Thus, the growth data for each population reflect the influence of five consecutive annual sets of climatic conditions.

We chose to use the Intergovernmental Panel on Climate Changes (IPCC) 1961–1990 climatic normals (available from the IPCC climate data distribution centre website: www.ipcc-data.org/obs/get_30yr_means.html), specific to the location for each population, to characterize the climatic conditions associated with the growth increments exhibited by each population. The following climate variables were used: ground frost frequency (days), precipitation (cm·day$^{-1}$), mean air temperature (°C), cloud cover (%), and solar radiation (W·m$^{-2}$). The IPCC 1960–1990 normal data sets consist of monthly mean values for the five variables at a resolution of 0.5° latitude by 0.5° longitude. The values for each variable were interpolated from weather station data using thin-plate splines (New et al. 1999). For each population location in the walleye database, an annual mean for each variable was calculated, and this location-specific set of five mean values was used to represent the climatic conditions experienced by that population over the period when the observed growth increments were generated.

We believe that these well-validated and readily available climatic data are sufficient for our purpose because almost all of the growth data sets in our database were collected prior to the onset of the warming trends that are ubiquitous in recent North American air temperature time series. Retrospectively, such trends typically begin in the late 1960s to early 1970s; however, they do not escape the historical range of variation set by the 1900–1970 period until at least the mid-1980s (e.g., Stott et al. 2000; Jones et al. 2006). Hence, we felt that the 1961–1990 normal values would reflect the spatial differences in climate that would largely be responsible for driving any systematic, climate-based differences in

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the growth patterns exhibited by the populations in our data set. We carried out the following tests of this assumption. First, we selected 8 locations, each representative of a geographically distinct group of populations in our growth database (one location for each of the glacial refugia AT, MP and HB; one location for the western half of MS; one location for the eastern half of MS; one location for each of the three regionally distinct groups of introduced populations). Second, for each population, we used the IPCC location-specific, historical air temperature time series database derived using the same methodology as was used to derive the 1961–1990 normal values (Mitchell et al. 2004) to estimate the annual air temperature at the reference location closest to the population for the decade immediately prior to the year when the growth data for the populations was reported. Third, we generated six group means from these decade-specific values by averaging across populations within each of the five refugium groups and by averaging across all of the introduced populations. Finally, we compared the decade-specific, reference site air temperatures with the 1961–1990 normal air temperatures for each group. We found that within each group, the spatial variation in air temperature between populations over a fixed time period (as measured by the standard deviation of the original 1961–1990 normal temperatures for the populations in the group) was typically two or three times greater than the temporal variation in air temperature associated with different growth time periods at the reference site for each group. This confirms our expectation that any associations between growth and climate in our data would be largely driven by the spatial variation in climate, captured in the 1961–1990 normal data. In addition, the within-group differences between these two temperature indices were small (<0.2 °C for the introduced populations and for three of the five refugia, including the east half of MS; about 0.6 °C for the west half of MS; and about 1.0 for HB); the two indices were highly correlated ($r^2 > 0.99$, $p < 0.001$) and followed a linear, 1:1 relationship (i.e., the slope was not significantly different from 1; $p > 0.1$); and the intercept was not significantly different from zero ($p > 0.1$). This is consistent with our hypothesis that at the regional level, the mean climate evident over the period of data collection was essentially identical with the mean climate characterized by the 1961–1990 climate normals.

### Statistical analysis of data

Incremental growth-at-age and climate data sets were standardized to $z$ scores before carrying out any further analysis to remove the effects of different scales of variables. Principal component analysis (PCA) was applied to increment-at-age and climate data sets to characterize the main trends of variation of the observations with respect to both growth and climate. A Procrustean randomization test (PROTEST: Jackson and Harvey 1993; Jackson 1995) was applied to the first two principal components from each data set. To find the maximum concordance between the two data matrices (i.e., relationship between the climate and the growth), PROTEST carries out rescaling, rotating, and (or) reflecting operations on the configurations of original data (the first two principal components from both data matrices in this study) to identify the closest fit between two matrices and then generates a standardized residual for each individual observation. It then tests whether this match is significantly different from random using a randomization test and then generates a standardized residual for each individual observation. The standardized residuals are used to rank each observation in terms of its fidelity to the overall pattern of association that PROTEST has identified between the two data sets (Jackson 1995; Olden et al. 2001).

Comparison of the direction and magnitude of the residual vectors from the Procrustes analysis can determine whether groups of observations exhibit similar deviations from the best matching pattern generated by the analysis. In this study, each residual vector was produced by subtracting the observed growth vector for each population (in the growth space determined by the first two principal component axes) from the corresponding growth vector predicted from the climatic conditions for that population. The predicted growth vector is just the climate vector mapped into growth PCA space by the Procrustes fit (i.e., a set of rescaling, rotating, and reflecting operations that maximize the concordance between the climate and growth data matrices). The four quadrants of the two-dimensional ordination plot, based on the first two principal component axes derived from the growth data, were used to classify each individual observation into one of four groups depending on the quadrant where the residual vector for the observation was located. The quadrant classification was assigned in a counterclockwise manner. For example, a population with its residual vector in quadrant 1 would have two positive components and a population with two negative components to its residual vector would be in quadrant 3. The assignment of individual residuals to four different quadrants can characterize the residual patterns among populations located in different refugium regions and help us understand the relationship between climate-based predicted values and observed values. A two-tailed $t$ test was used to compare the magnitude of residual vectors between different population groupings: (*i*) populations located outside the native range (subsequently referred to as introduced populations) versus populations located within the native range (subsequently referred to as native populations); and (*ii*) among native populations, grouping based on the glacial refugium associated with the location of the populations. A $\chi^2$ test was applied to each group to test for a nonrandom distribution of residual vectors among the four quadrants in the growth ordination plot. Finally, a Procrustean superimposition plot was used to illustrate how the observed growth for each group differed from the expected growth based on the PROTEST best match pattern (Peres-Neto and Jackson 2001).

Simulation studies have shown that PROTEST is superior to the Mantel test in assessing the association between two multivariate data matrices (Peres-Neto and Jackson 2001). The standard PROTEST is based on the least-squares criterion, which is adversely affected by atypical observations (Olden et al. 2001) as in standard linear regression analyses. Therefore, a resistant-fit approach, using the repeated-medians algorithm, was applied to reduce the influence of atypical observations in the data set (Siegel and Benson 1982; Olden et al. 2001).

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**Table 1.** The eigenvector coefficients and eigenvalues for the first two principal components (PCs) from principal component analysis (PCA) of walleye (*Sander vitreus*) incremental growth data.

| Variable | PC1 | PC2 |
|---|---|---|
| Growth | | |
| Increment at age 1 | 0.082 | 0.792 |
| Increment at age 2 | –0.437 | 0.549 |
| Increment at age 3 | –0.536 | 0.016 |
| Increment at age 4 | –0.545 | –0.152 |
| Increment at age 5 | –0.466 | –0.216 |
| Eigenvalue | 1.789 | 1.243 |
| Percentage (%) | 35.79 | 24.86 |
| Climate | | |
| Frost frequency | 0.543 | 0.080 |
| Precipitation | –0.406 | –0.439 |
| Temperature | –0.541 | 0.033 |
| Radiation | –0.496 | 0.352 |
| Cloud cover | 0.036 | –0.822 |
| Eigenvalue | 3.251 | 1.355 |
| Percentage (%) | 65.02 | 27.11 |

## Results

For the growth data set, the first principal component represents walleye average growth rate after age 1, because the PCA coefficients of standardized increment-at-age variables for ages 2–5 are similar to one another in sign and magnitude (Table 1). Age 1 growth was generally unrelated to this first component given its small PCA coefficient (0.082). However, for the second principal component, the absolute values of the coefficients for increment at age 1 (0.792) and increment at age 2 (0.549) were more than twice as large as the ones for the increments at older ages. This indicates that the second principal component was most influenced by the early growth rate. The PCA analysis showed that walleye early growth rate and average young adult growth rate, as summarized by the second and first PCA components, composed 60.65% (24.86% and 35.79%, respectively) of the total variation in annual increment-at-age of walleye in North American lakes.

For the climate data set, the first principal component contrasted frost frequency with precipitation, temperature, and solar radiation. Cloud cover had little influence on this component, given the low value (0.036) for its coefficient in the component (Table 1). The second principal component contrasted solar radiation with both precipitation and cloud cover. The first two components accounted for about 92.13% of the total variation in the climate data (65.02% and 27.11%, respectively). The climatic conditions for introduced walleye populations exhibited extreme or close to extreme values for at least one of the climate principal components and effectively bounded the climate PCA space inhabited by the native populations (Fig. 2).

Results from the resistant-fit PROTEST analysis showed that the walleye increment-at-age ordination was significantly associated with the ordination of the climatic conditions ($m^2 = 0.800$, $p = 0.002$). The vector residuals from the analysis can be used to assess the degree to which each population fit the overall association between walleye increment-at-age and climatic conditions. The population with the largest residual (i.e., Lake Meridith, Texas, in Appendix A) exhibited growth and climatic characteristics that were least consistent with the overall association between growth and climate, whereas the population with the smallest residual (i.e., Attawapiskat Lake, Ontario, in Appendix A) exhibited the growth and climatic characteristics that were most consistent with the overall association. The residual obtained for Lake Meridith was so different (i.e., twice as much as the second largest residuals and six times as much as the average residual values of the remaining 88 populations) from all others that it is considered independently of the others. The remaining 88 populations were divided into four groups with an equal number of 22 populations in each group, based on their rank-ordered residuals (Appendix B, Fig. B1). Groups 3 and 4 were the populations with the poorest match, whereas groups 1 and 2 had the best match. The Lake Meridith population was placed alone in group 5 (Appendix B, Fig. B1). Most populations that exhibit a good match between growth and climate are located in the central region of North America: western South Dakota, Iowa, Minnesota, and northwestern Ontario. Regions surrounding this well-matched group exhibited a relatively poor match between walleye growth pattern and climatic conditions (Fig. 3). Residual magnitudes for introduced populations were significantly larger than those for the populations in the native range (*t* test, $t_{15} = -3.96$, $p = 0.001$). This finding suggests that the overall association between climatic conditions and growth pattern is shaped largely by populations within the native range for walleye and that it does not hold for introduced populations outside the native range.

Comparing populations within the native range, nearly half the populations exhibiting a close growth–climate rela-

**Fig. 2.** Biplot of the first two principal component (PC) scores for climate conditions showing difference of climate conditions for the introduced populations (triangles) and the native populations (circles). The labels in the figure are the population ID numbers provided in Appendix A.

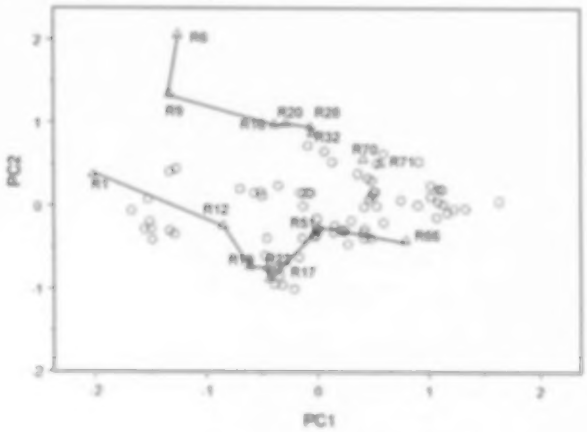


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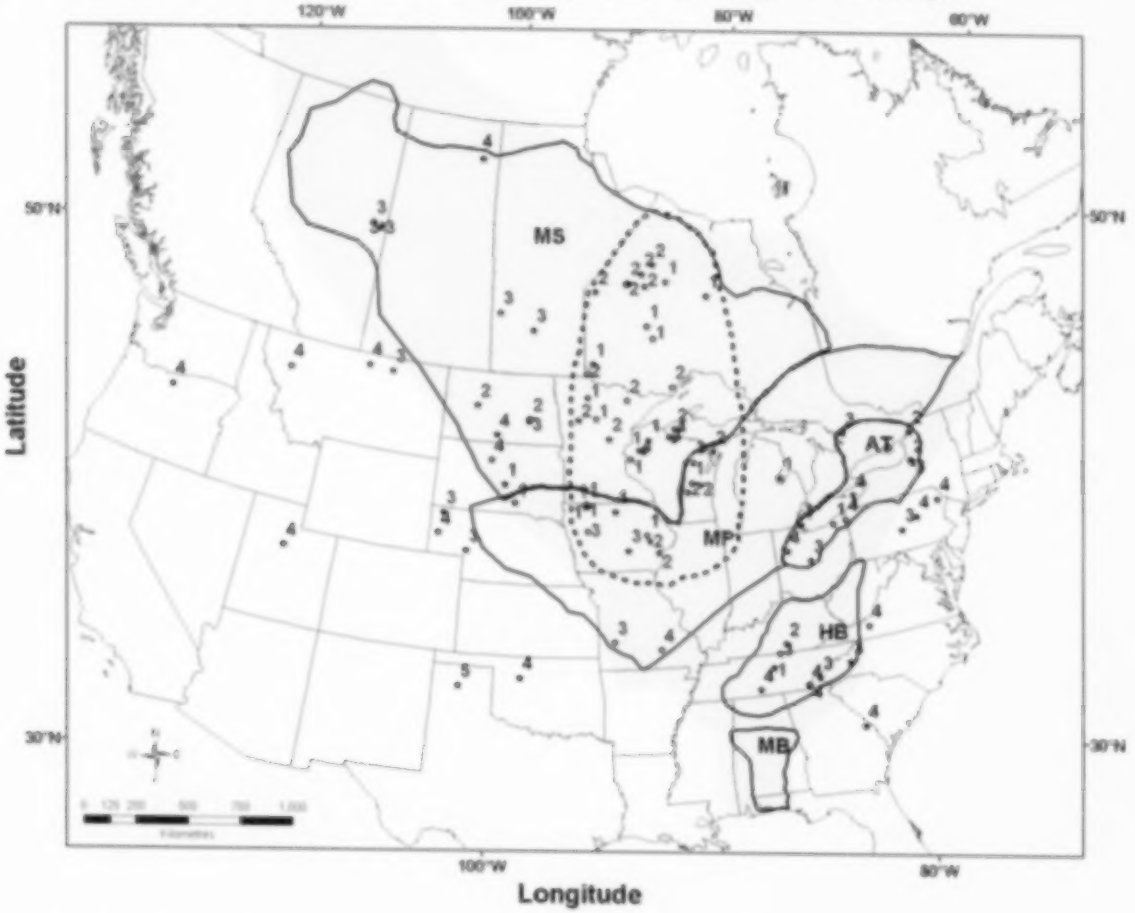
**Fig. 3.** A map of rank groups of residuals of individual walleye (*Sander vitreus*) populations from Procrustes analysis. Numbers designate the rank groups in Appendix B, Fig. B1. The lower the number for the rank group (e.g., 1 vs. 2), the better the concordance between climate conditions and walleye growth. The shaded area shows walleye native distribution (redrawn from Colby et al. 1979); populations enclosed by the thick, broken line compose the majority of the population with high concordance. AT, Atlantic refugium; MS, Missouri refugium; MP, Mississippi refugium; HB, hybrids from MS and MP; MB, Mobile Basin drainage.




tionship (i.e., those from residual groups 1 and 2) are located in the region colonized from the MP refugium (Fig. 3), whereas the remaining half are located in Minnesota and north-western Ontario (Fig. 3 and region MS2 in Fig. 4). Billington (1996) suggested that this latter region (MS2 in Fig. 4) was colonized from the MS refugium; however, this classification is questionable because (*i*) the Minnesota populations exhibit allele frequencies that are similar to populations attributed to the MP refugium; and (*ii*) the sample size from northwestern Ontario is small ($N < 5$) (Billington et al. 1992). A majority of populations from the AT refugium region (Fig. 3), the remainder from the MS refugium region (MS1 in Fig. 4), and the populations from the hybrid region (HB in Fig. 3) did not follow the same walleye climate–growth relations shaped by the MP and MS2 regions and therefore exhibited large residuals (in groups 3 and 4) from the general relationship. The residuals for the populations from the MP and MS2 regions were significantly smaller than the residuals for the populations from the AT, MS1, and HB regions (*t* test, $t_{48} = -4.96$, $p < 0.001$).

The dominant direction of the residuals also differed among populations from regions with different genetic histories (Fig. 4). The null hypothesis of a uniform distribution of residual directions among the four quadrants was rejected for populations from the MS1 ($\chi^2_3 = 8.67$, $p = 0.03$) and HB ($\chi^2_3 = 9.57$, $p = 0.02$) regions; residuals from the MS1 region tended to lie in the third and fourth quadrants, while residuals from the HB region tended to lie in the second quadrant (Fig. 4, Appendix Fig. B2). The distribution of residual directions for population from the AT region was skewed to the first quadrant (Fig. 4, Appendix Fig. B2), but was not significantly different from uniform ($\chi^2_3 = 4.4$, $p = 0.22$). However, the power of this particular test was low because the sample size was small (total 10 populations). With a sample size of 10, the power to detect a 20% departure from the null hypothesis is only 0.075 (i.e., with a sample of size

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**Fig. 4.** A map of directions of residuals of individual walleye (*Sander vitreus*) populations from Procrustes analysis and five genetically distinct groups. Numbers (1, 2, 3, 4) show quadrants where the residuals are located, quadrant 1 being the top-right quadrant and progressing counterclockwise. Polygons with thick lines show groups of genetically distinct populations; the broken line is a proposed separating line of Missouri refugium (MS) based on this study. The shaded area is same as the circled area in the broken line in Fig. 3. AT, Atlantic refugium; MS1 and MS2, Missouri refugium; MP, Mississippi refugium; HB, hybrids from MS and MP; MB, Mobile Basin drainage.

of 10 and at the 5% significance level, there is only a 7.5% probability of detecting at least a 20% shift from the uniform distribution). The distribution of residual directions was not significantly different from uniform for populations from the MP region ($\chi^2_3 = 3.53$, $p = 0.32$) and for populations from the MS2 region ($\chi^2_3 = 2.91$, $p = 0.41$). Therefore, both the residual direction pattern (i.e., uniform distribution among the four quadrants) and residual magnitude (low rank) for populations from the MP and MS2 regions were similar. A uniform distribution of residual directions was also evident for populations located outside the native range of the species ($\chi^2_3 = 1.27$, $p = 0.73$) (Appendix Fig. B2).

The superimposition plots (Fig. 5) demonstrate how observed growth differs from expected or predicted growth, given the observed climatic conditions. For example, a population with the residual vector (***a***) in Fig. 5*a* exhibits a lower observed adult growth rate than was predicted by the climatic conditions experienced by the population because the vector (***a***) is largely parallel to the eigenvectors for young adult growth (primarily increments 3, 4, and 5) that make up the first principal component (PC 1), and it points from an observed position of lower adult growth on PC 1 to a predicted position of higher adult growth on PC 1. Similarly, the population with residual vector (***b***) in Fig. 5*a* exhibits a lower observed early growth than predicted from the climatic conditions it experienced, because vector (***b***) is almost parallel to the eigenvectors for early life growth (primarily ages 1 and 2) that largely make up PC 2, and it points from an observed position of lower early growth to a predicted position of higher early growth. The residual vectors for populations from the regions MP and MS2 were relatively small in magnitude and did not exhibit a dominant direction (Fig. 5*b* and Fig. 5*c*). However, populations from the regions associated with the other three refugia produced larger residuals that exhibited dominant directions: (*i*) among populations from the MS refugium region (Fig. 5*e*), early growth rate

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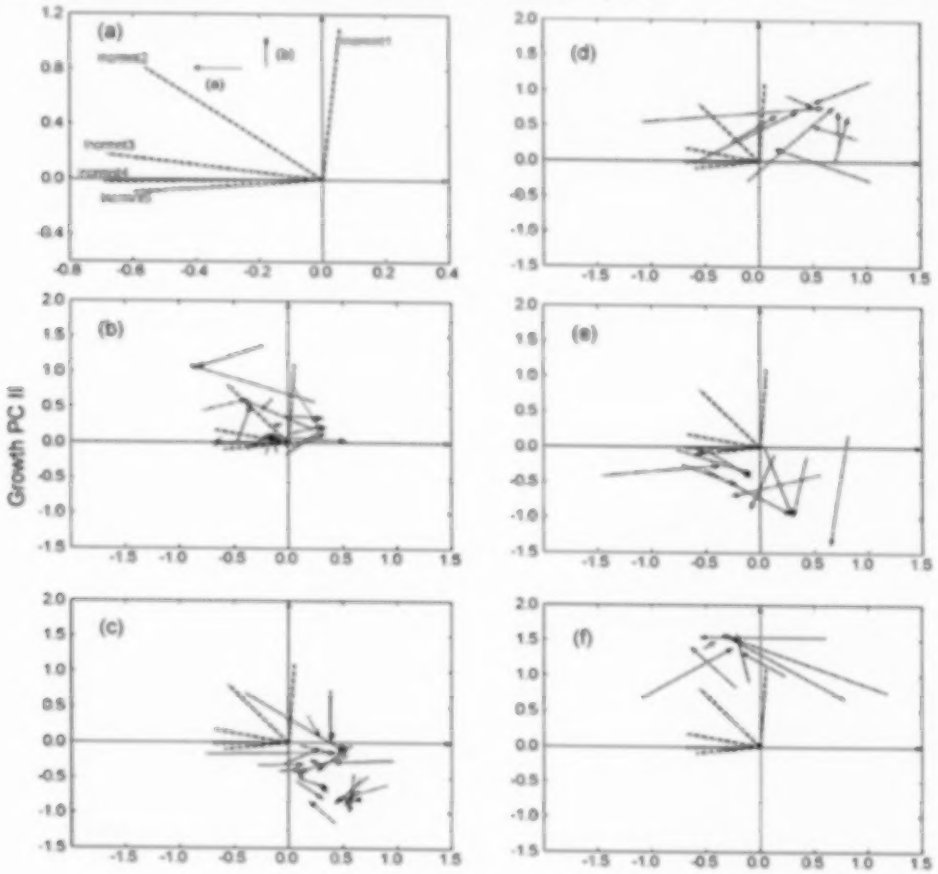
**Fig. 5.** Superimposition plot of five growth eigenvectors (broken lines) and residuals for the populations located in different refugium regions: (*a*) example; (*b*) MP (Mississippi refugium); (*c*) MS2 (Missouri refugium 2); (*d*) AT (Atlantic refugium); (*e*) MS1 (Missouri refugium 1); (*f*) HB (hybrids from MS and MP). Refer to the text for more detail. In the Example panel, the direction of residual (***a***) is parallel to the principle component that characterizes young adult (ages 3, 4, and 5) growth, thus indicating that the populations with this residual exhibited a smaller observed young adult growth rate than expected given its climatic conditions; a similar explanation applies to residual (***b***) in the example and to all the residuals in the other five panels.




tended to be higher than expected; (*ii*) among populations from the HB region (Fig. 5*f*), both early and later growth rates were lower than expected; and (*iii*) among populations from the AT refugium region (Fig. 5*d*), early growth rate tended to be lower than expected, while growth in later life tended to be higher than expected.

## Discussion

Significant relationships between life history traits and environmental factors are caused by phenotypic plasticity responding to environmental gradients and (or) by natural selection (Pigliucci 2001). A relationship based solely on phenotypic plasticity should apply consistently across the geographic distribution of a species, as long as the values for the environmental factors that drive the relationship remain within the range over which well-defined phenotypic responses have developed. The current patchy geographic distribution of walleye genotypes is the outcome of postglacial colonization from multiple refugia coupled with continuing spatial isolation of the different refugial groupings (Billington 1996). Therefore, we expect that walleye populations from the same genetic region will carry similar refuge-specific genotypes, whereas walleye populations from different genetic regions will carry the different genotypes associated with those regions. It is expected that such genetic variation may account for at least some of the phenotype variation.

The lack of concordance between observed and expected somatic growth for introduced populations, given their climatic conditions, suggests that either the introduced populations have not been established long enough to adapt to the environmental conditions in their new locations, or the extreme environmental conditions in those locations are outside the range over which a well-defined plastic response

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has developed. The latter possibility is consistent with the fact that most introduced populations lie at or outside the boundaries of the climate space defined by the native distribution of the species, and it is the climate space of the native populations that would most likely have set the boundaries over which a well-defined phenotypic response could develop (Dunlop and Shuter 2006). In addition, given that the introduced populations likely derive from a variety of sources, a random distribution for the direction of their residual vectors is expected and was observed. The vector direction for each introduced population tends to match the dominant direction found among the residual vectors in its neighbouring refugial group. This suggests that introductions largely derive from nearby native stocks.

In evolutionary ecology and genetics, the terms norm of reaction or reaction norm are used to describe how a genotype is expressed by different phenotypes across a range of environmental conditions (Pigliucci 2001). The decreasing concordance between climate and walleye growth, from the centre of the native distribution to the edges of the current distribution, may indicate that walleye climate–growth reaction norms vary across the current geographic range of the species. Genotypic variation among walleye populations in the native range could be the cause of variation in the walleye climate–growth reaction norm. In our study, the concordance between walleye growth and climate identified by the PROTEST analysis is shaped primarily by populations located in the region colonized from the MP refugium and from the populations located in western Ontario and Minnesota populations (i.e., MP–MS2). It is possible that this climate–growth linkage reflects a single reaction norm, common to this genetically similar group of populations. Populations located in the three other geographic regions (i.e., AT, MS1, and HB) that were identified as genetically distinct from each other and from the MP–MS2 region by Billington et al. (1992), Billington and Strange (1995), and Billington (1996) also exhibited large deviations from the MP–MS2 climate–growth reaction norm. In addition, the directions of the vector residuals from the populations within each of these regions (i.e., AT, MS1, and HB) exhibited a common direction, and that common direction differed among regions. These findings are consistent with the hypothesis that the walleye climate–growth reaction norm differs systematically among populations with different postglacial colonization histories.

Other fish species have been shown to exhibit genetic-based differences in the reaction norm linking the response of life history traits to changes in environmental factors. Yamahira and Conover (2003) compared the effect of water temperature on growth rate in northern and southern populations of Atlantic silverside (*Menidia menidia*). They found a significant difference in the temperature–growth reaction norm between northern and southern populations, and they also found that this difference had a strong genetic basis. In young-of-the-year walleye, common garden experiments (Galarowicz and Wahl 2003) point to the presence of a strong genetic component in the significant differences in metabolic rate, food consumption, food conversion efficiency, and growth observed among stocks from different geographic regions that cross the boundaries of several glacial refugia, likely across two or more regions that were genetically distinguishable.

Because this study and other studies mentioned above suggest that genetic variation is a likely cause of variation in fish growth – environment reaction norms, our finding that populations from region MP and MS2 exhibit similar vector residuals (both in direction and magnitude) suggests that populations from the MS2 region could be more closely linked to the MP refugium populations rather than to the MS refugium populations as suggested by Billington (1996). Resolution of this issue would require more intense genetic work on populations in the MS2 region. Similarly, our hypothesis that different walleye phylogeographic lineages exhibit different growth–environment reaction norms requires further testing, ideally through a program of common garden studies.

In conclusion, climatic conditions significantly influence walleye growth patterns across their geographic range; however, the response of walleye growth to climate differs among groups of populations that exhibit evidence of genetic divergence. For most fish species, somatic growth is significantly related to other life history traits, such as fecundity and maturation. Those traits, therefore, would also be expected to show similar divergent patterns among those groups. These considerations suggest that caution should be taken when assessing possible effects of climate variation and climate change on the life history traits of different walleye populations (e.g., Shuter et al. 1998), especially when such assessments include several genetically distinct groups of walleye. Similar concerns would likely apply to other fish species that exhibit substantial genetic diversity within their zoogeographic ranges.

Our analysis demonstrates the effectiveness of the Procrustes approach to characterize and test how a multivariate set of response variables changes in response to generalized changes in a multivariate set of independent variables. While King and Jackson (1999) showed the use of PCA and Procrustes analysis in relating climate data to aquatic systems, we have extended its use in examining life history relationships. The Procrustes framework imposes relatively few restrictions on the shape of the response relationship and naturally accommodates a multivariate characterization of both response variables and independent variables — it integrates the individual response of each dependent variable into a comprehensive picture of an overall pattern of response to extensive changes in a set of independent variables. In our analysis, the resistant-fit Procrustes characterization of the concordance between a multivariate set of biological response variables (e.g., fish growth increment) and a multivariate set of environmental independent variables (e.g., climatic conditions) permitted us to identify groups of populations that exhibited not only a common response to environmental variation within each group, but also significant differences among groups in the common response specific to each group. Thus, the resistant-fit version of Procrustes can be effective in identifying heterogeneity in the response pattern among different subsets of the data, as well as in identifying an overall pattern of response.

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Appendices A and B appear on the following pages.

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## Appendix A

**Table A1.** Locations, residual groups (rank and direction) from PROTEST and walleye origin of the lakes in North America.

| ID No. | Lake name | State or province* | Latitude (°N) | Longitude (°W) | Reference† | Rank‡ | Direction§ | Refugium¶ |
|---|---|---|---|---|---|---|---|---|
| R1 | Barton Reservoir | GA | 33.09 | 81.87 | 1 | 4 | 2 | Introduced |
| R2 | Hiwassee Reservoir | NC | 35.11 | 84.14 | 1 | 4 | 2 | HB |
| R3 | Apalachia Lake | NC | 35.12 | 84.16 | 1 | 4 | 2 | HB |
| R4 | Norris Reservoir | TN | 35.23 | 86.57 | 1 | 4 | 2 | HB |
| R5 | Nantahala Reservoir | NC | 35.35 | 83.57 | 1 | 3 | 2 | HB |
| R6 | Lake Meridith | TX | 35.64 | 101.66 | 1,2 | 5 | 3 | Introduced |
| R7 | James Reservoir | NC | 35.75 | 81.92 | 1 | 3 | 2 | HB |
| R8 | Center Hill Reservoir | TN | 36.05 | 85.76 | 1,2 | 1 | 1 | HB |
| R9 | Canton Reservoir | OK | 36.13 | 98.61 | 1 | 4 | 3 | Introduced |
| R10 | Dale H. Reservoir | TN | 36.61 | 85.32 | 1 | 3 | 1 | HB |
| R11 | Cumberland | KY | 36.96 | 84.94 | 1 | 2 | 2 | HB |
| R12 | Claytor Reservoir | VA | 37.07 | 80.60 | 1 | 4 | 4 | Introduced |
| R13 | Current River | MO | 37.25 | 91.35 | 2 | 4 | 2 | MP |
| R14 | Stockton Lake | MO | 37.64 | 93.76 | 1 | 3 | 3 | MP |
| R15 | Hoover Reservoir | OH | 40.17 | 82.87 | 1 | 3 | 3 | AT |
| R16 | Utah Lake | UT | 40.20 | 111.79 | 2 | 4 | 3 | Introduced |
| R17 | Juniata River | PA | 40.58 | 77.59 | 2 | 3 | 1 | Introduced |
| R18 | Ferguson Reservoir | OH | 40.74 | 84.04 | 1 | 4 | 1 | AT |
| R19 | Susquehanna River | PA | 40.97 | 76.64 | 2 | 4 | 1 | Introduced |
| R20 | McConaughy Reservoir | NE | 41.26 | 101.84 | 1 | 3 | 3 | Introduced |
| R21 | Mississippi River | IA | 41.29 | 91.09 | 1 | 2 | 1 | MP |
| R22 | Lake Wallenpaupack | PA | 41.41 | 75.23 | 2 | 4 | 1 | Introduced |
| R23 | Des Moines River | IA | 41.46 | 92.79 | 1 | 3 | 2 | MP |
| R24 | BeaverCreek Reservoir | OH | 41.52 | 81.22 | 1 | 1 | 4 | AT |
| R25 | Pymatuning Lake | PA | 41.60 | 80.51 | 2 | 4 | 1 | AT |
| R26 | Lake Erie (western) | GL | 41.75 | 83.00 | 1,2 | 3 | 1 | AT |
| R27 | McBride Lake | IA | 41.80 | 91.56 | 1 | 2 | 1 | MP |
| R28 | Minature Reservoir | NE | 41.93 | 103.49 | 1 | 4 | 4 | Introduced |
| R29 | Cedar River | IA | 42.08 | 91.73 | 1 | 1 | 3 | MP |
| R30 | Black Hawk Lake | IA | 42.30 | 95.05 | 1 | 3 | 2 | MP |
| R31 | Lake Erie (eastern) | GL | 42.50 | 79.75 | 1 | 4 | 1 | AT |
| R32 | Whitney Reservoir | NE | 42.78 | 103.31 | 1 | 3 | 2 | Introduced |
| R33 | Clear Lake | IA | 43.13 | 93.43 | 1,2 | 1 | 1 | MP |
| R34 | Oneida Lake | NY | 43.20 | 75.91 | 1 | 3 | 1 | AT |
| R35 | Scriba Creek | NY | 43.31 | 76.02 | 2 | 2 | 2 | AT |
| R36 | West Okoboji Lake | IA | 43.39 | 95.18 | 1,2 | 1 | 2 | MP |
| R37 | East Okoboji Lake | IA | 43.39 | 95.09 | 2 | 1 | 2 | MP |
| R38 | Okoboji Lake | IA | 43.39 | 95.16 | 1 | 1 | 1 | MP |
| R39 | Francis Case | SD | 43.45 | 99.28 | 1 | 1 | 3 | MP |
| R40 | Spirit Lake | IA | 43.48 | 95.10 | 2 | 1 | 1 | MP |
| R41 | Puckaway Lake | WI | 43.76 | 89.17 | 1 | 2 | 4 | MP |
| R42 | Saginaw Bay | MI | 43.83 | 83.67 | 1 | 1 | 4 | MP |
| R43 | Winnebago Lake | WI | 44.04 | 88.41 | 1 | 2 | 1 | MP |
| R44 | Lake Poygon | WI | 44.15 | 88.83 | 1 | 1 | 1 | MP |
| R45 | Sharpe | SD | 44.20 | 99.93 | 1 | 1 | 3 | MS1 |
| R46 | Black Lake | NY | 44.50 | 75.61 | 1 | 2 | 2 | AT |
| R47 | Wolf River | WI | 45.02 | 88.65 | 2 | 3 | 4 | MP |
| R48 | 3 Mile Lake | ON | 45.18 | 79.46 | 1 | 3 | 2 | AT |
| R49 | Oahe (SD) | SD | 45.20 | 100.80 | 1 | 4 | 1 | MS1 |
| R50 | Pike Lake | WI | 45.32 | 92.37 | 1 | 1 | 4 | MS2 |
| R51 | John Day Reservoir | OR | 45.33 | 120.54 | 1 | 4 | 4 | Introduced |
| R52 | North Green Bay | GL | 45.38 | 87.38 | 1 | 2 | 1 | MP |
| R53 | Red Cedar River | WI | 45.61 | 91.59 | 1 | 1 | 3 | MS2 |
| R54 | Ripley Lake | WI | 45.71 | 91.85 | 1 | 3 | 4 | MS2 |
| R55 | Trout Lake | WI | 46.03 | 89.67 | 1 | 4 | 1 | MS2 |
| R56 | Clear Lake | WI | 46.10 | 91.24 | 1 | 1 | 2 | MS2 |
| R57 | Bass Lake | WI | 46.19 | 89.96 | 1 | 4 | 4 | MS2 |
| R58 | Mile Lacs Lake | MN | 46.23 | 93.63 | 1 | 2 | 1 | MS2 |
| R59 | Oahe (ND) | ND | 46.29 | 100.58 | 1 | 4 | 4 | MS1 |

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**Table A1** (*concluded*).

| ID No. | Lake name | State or province* | Latitude (°N) | Longitude (°W) | Reference† | Rank‡ | Direction§ | Refugium¶ |
|---|---|---|---|---|---|---|---|---|
| R60 | Lake Gogebic | MI | 46.52 | 89.58 | 2 | 2 | 4 | MS2 |
| R61 | Jamestown Reservoir | ND | 46.96 | 98.62 | 1,2 | 3 | 4 | MS1 |
| R62 | Many point Lake | MN | 47.06 | 95.54 | 2 | 2 | 1 | MS2 |
| R63 | Spiritwood Lake | ND | 47.07 | 98.59 | 1,2 | 2 | 4 | MS1 |
| R64 | Leech Lake | MN | 47.14 | 94.40 | 1 | 1 | 2 | MS2 |
| R65 | Lake Sakakawea | ND | 47.52 | 101.89 | 1 | 2 | 4 | MS1 |
| R66 | Rainbow Lake | MT | 47.68 | 113.95 | 2 | 4 | 4 | Introduced |
| R67 | Lake Vermillion | MN | 47.89 | 92.42 | 1 | 2 | 3 | MS2 |
| R68 | Red Lake | MN | 48.06 | 94.92 | 1 | 1 | 1 | MS2 |
| R69 | Kaministiquia River | ON | 48.35 | 89.45 | 3 | 2 | 3 | MS2 |
| R70 | Nelson Reservior | MT | 48.48 | 107.57 | 2 | 3 | 1 | Introduced |
| R71 | Milk River | MT | 48.57 | 109.12 | 2 | 4 | 4 | Introduced |
| R72 | Lake of Woods | MN | 49.07 | 94.90 | 1,2 | 2 | 3 | MS2 |
| R73 | Sandy Lake | ON | 49.50 | 94.53 | 2 | 1 | 2 | MS2 |
| R74 | Savanne Lake | ON | 50.50 | 90.43 | 2 | 1 | 4 | MS2 |
| R75 | Lake Manitoba | MB | 50.93 | 98.53 | 1 | 3 | 3 | MS1 |
| R76 | Lake St. Joseph | ON | 51.06 | 90.80 | 2 | 1 | 2 | MS2 |
| R77 | West Blue Lake | MB | 51.61 | 100.92 | 1 | 3 | 3 | MS1 |
| R78 | Attawapiskat Lake | ON | 52.14 | 86.43 | 2 | 1 | 3 | MS2 |
| R79 | Deer Lake | ON | 52.66 | 94.25 | 2 | 2 | 2 | MS2 |
| R80 | North Caribou Lake | ON | 52.82 | 90.71 | 2 | 2 | 3 | MS2 |
| R81 | Winnummin Lake | ON | 52.94 | 89.18 | 2 | 1 | 3 | MS2 |
| R82 | Petownikip Lake | ON | 52.94 | 92.04 | 2 | 2 | 4 | MS2 |
| R83 | Sakwaso Lake | ON | 53.02 | 91.91 | 2 | 2 | 3 | MS2 |
| R84 | Makoop Lake | ON | 53.38 | 90.86 | 2 | 2 | 3 | MS2 |
| R85 | Big Trout Lake | ON | 53.76 | 90.00 | 2 | 2 | 3 | MS2 |
| R86 | Ethel Lake | AB | 54.53 | 110.35 | 1 | 3 | 4 | MS1 |
| R87 | Marie Lake | AB | 54.63 | 110.30 | 1 | 3 | 4 | MS1 |
| R88 | Wolf Lake | AB | 54.68 | 110.97 | 1 | 3 | 3 | MS1 |
| R89 | Wollaston Lake | SA | 58.28 | 103.28 | 1 | 4 | 3 | MS1 |

*State or province abbreviations follow postal abbreviations.
†1, Carlander 1997; 2, Colby et al. 1979; 3, Stephenson and Momot 1991.
‡1, 2, 3, 4, 5: residual rank groups from PROTEST (Fig. 2).
§1, 2, 3, 4: four quadrants for residual direction group.
¶Refugia of origin of walleye populations (Fig. 4): Introduced, the introduced populations.

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Stephenson, S.A., and Momot, W.T. 1991. Food habitat and growth of walleye, *Stizostedion vitreum*, smallmouth bass, *Micropterus dolomieui*, and northern pike, *Esox lucius*, in the Kaministiquia River, Ontario. Can. Field-Nat. **105**: 517–521.

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## Appendix B

**Fig. B1.** Magnitude of standardized vector residuals from PROTEST analysis and the groups assigned based on their rank orders. The number beside the bar indicates the populations ID number in Appendix A. Low ranks indicate the better match between climate conditions and walleye (*Sander vitreus*) growth.

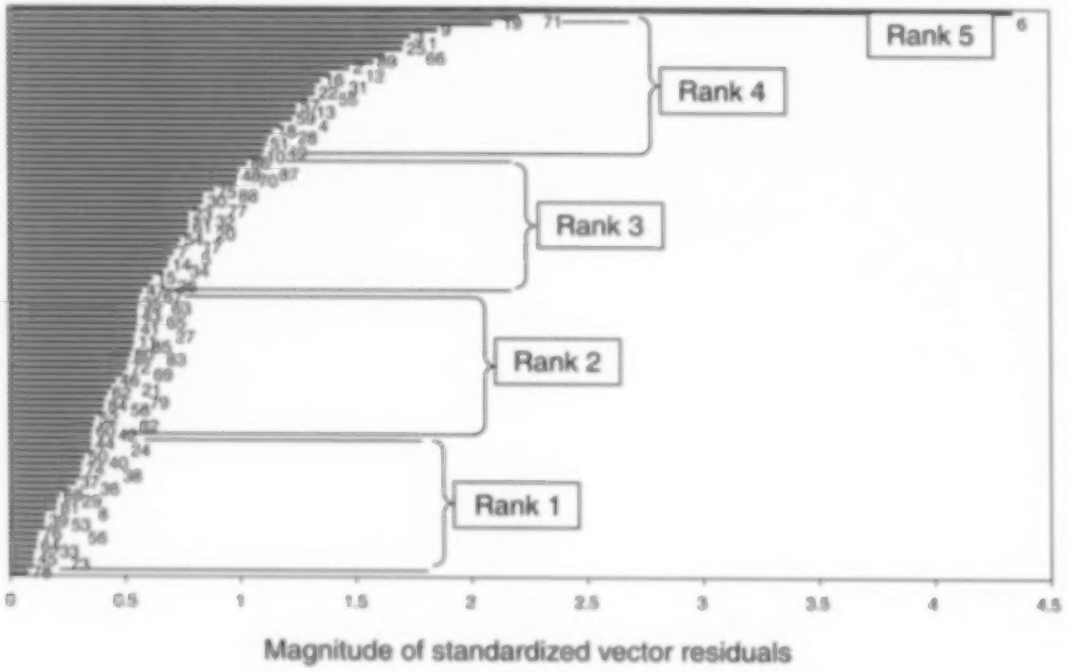


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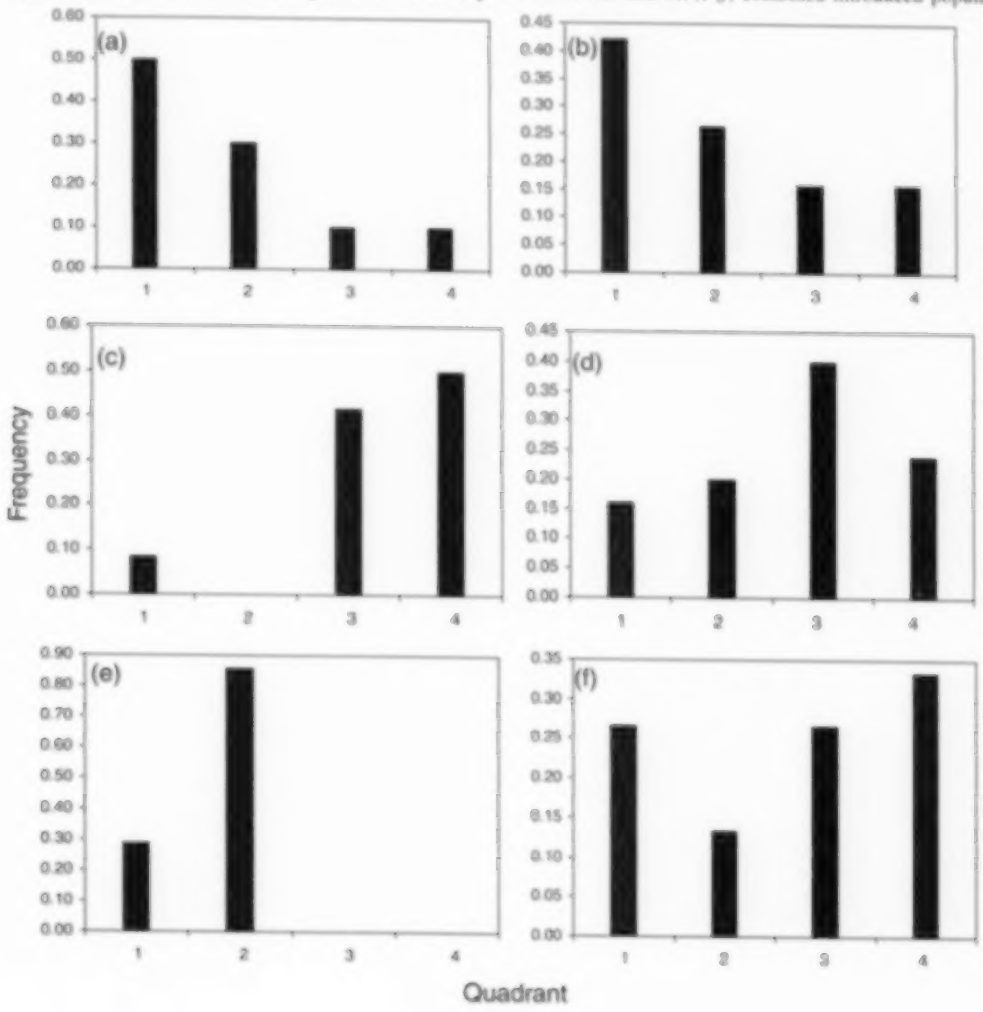
**Fig. B2.** The frequency of directions of vector residuals from PROTEST analysis from each genetically distinct group (*a*–*f*) showing distinct characteristics of the vector directions within each group. (*a*) AT (Atlantic refugium); (*b*) MP (Mississippi refugium); (*c*) MS1 (Missouri refugium 1); (*d*) MS2 (Missouri refugium 2); (*e*) HB (hybrids from MS and MP); (*f*) combined introduced populations.

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# Evaluation of visual survey methods for monitoring Pacific salmon (*Oncorhynchus* spp.) escapement in relation to conservation guidelines

**Kendra R. Holt and Sean P. Cox**

**Abstract:** Canada's Wild Salmon Policy requires that biological status of conservation units of Pacific salmon (*Oncorhynchus* spp.) be assessed regularly in relation to abundance-based benchmarks. Visual survey methods, in which periodic counts of spawning fish are made throughout a season, will likely be used for this purpose because they provide a cost-effective means of monitoring interannual trends in escapement. Trend detection performance for visual survey methods depends mainly upon consistency in (*i*) the ability of observers to detect fish and (*ii*) the annual timing of fish presence in the survey area. We developed a Monte Carlo simulation procedure to evaluate the ability of four visual survey methods (peak count, mean count, trapezoidal area-under-the-curve (AUC), and likelihood AUC) to detect 30% declines in coho salmon (*Oncorhynchus kisutch*) escapement over 10 years (i.e., the magnitude of trend that would warrant listing a coho population as threatened using the listing criteria of the Committee on the Status of Endangered Wildlife in Canada (COSEWIC)) given realistic levels of variability in these two factors. The mean count outperformed all other approaches across a wide range of scenarios about true population dynamics and survey designs, suggesting that a simple mean count method is suitable for monitoring coho escapements in relation to COSEWIC guidelines.

**Résumé :** La politique canadienne concernant le saumon sauvage exige que le statut des unités de conservation des saumons du Pacifique (*Oncorhynchus* spp.) soit évalué à intervalles réguliers par rapport à des niveaux d'abondance de référence. Pour réaliser cet objectif, on utilisera vraisemblablement des méthodes visuelles d'inventaire (dénombrements périodiques des poissons en fraie au cours d'une saison) parce qu'elles procurent un moyen avec un rapport rendement/coût intéressant pour suivre les tendances de l'échappement d'une année à l'autre. L'efficacité de la détection des tendances dans les méthodes visuelles d'inventaire dépend surtout de l'uniformité (*i*) de la capacité des observateurs à détecter les poissons et (*ii*) du calendrier de la présence des poissons dans la zone d'inventaire. Nous avons mis au point une procédure de simulation de Monte Carlo pour évaluer la capacité de quatre méthodes visuelles d'inventaire (dénombrement maximal, dénombrement moyen, surface trapézoïdale sous la courbe (AUC) et vraisemblance de AUC) à détecter des déclins de 30 % dans l'échappement de saumons coho (*Oncorhynchus kisutch*) sur 10 ans (soit une tendance suffisamment importante pour considérer la population de saumons coho comme menacée selon les critères du Comité sur la situation des espèces en péril au Canada (COSEPAC – COSEWIC)) avec des niveaux de variabilité réalistes de ces deux facteurs. Le dénombrement moyen fonctionne mieux que toutes les autres méthodes dans une gamme étendue de scénarios concernant la dynamique réelle de la population et les plans d'inventaire; cela indique qu'une méthodologie de dénombrement moyen est adéquate pour suivre les échappements de saumons coho selon les directives du COSEWIC.

[Traduit par la Rédaction]

## Introduction

Visual survey methods, in which observers periodically count fish throughout the spawning season, provide a cost-effective means of assessing interannual trends in Pacific salmon (*Oncorhynchus* spp.) escapement. Extensive survey programs that utilize visual survey methods allow a wide range of populations to be monitored; however, annual escapement estimates are generally assumed to be less certain than those obtained using more effort-intensive methods, such as enumeration fences or mark–recapture programs. Under Canada's new Wild Salmon Policy (WSP), genetically and geographically similar spawning aggregations of Pacific salmon will be grouped into conservation units (CUs), and for each CU, a monitoring plan will be developed to assess interannual trends in spawning escapement

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and the distribution of fish within the CU (DFO 2005). Extensive survey programs will likely be an important component of WSP monitoring plans.

Visual surveys have been used since the 1950s; however, the estimation methods applied to visual survey data have become increasingly complex. The peak count method, in which the highest count value observed in a spawning season is used to index escapement, was one of the earliest indices used (Bevan 1961) and is still widely used among management agencies (e.g., Geiger and McPherson 2004). Development of the trapezoidal area-under-the-curve (T-AUC) method (Ames and Phinney 1977; English et al. 1992) provided a means to estimate absolute escapement by incorporating information on survey life (the length of time fish remain alive in the survey area) and observer efficiency (the proportion of fish seen by observers) into the estimation procedure. Evaluations of the T-AUC method have shown that the accuracy of escapement estimates is highly dependent on year- and stream-specific estimates of survey life and observer efficiency (English et al. 1992; Irvine et al. 1992; Bue et al. 1998), which in themselves can be costly to obtain. More recently, a likelihood approach to AUC escapement estimation (L-AUC) has been proposed that allows uncertainty in survey life, observer efficiency, and the arrival timing of fish into the survey area to be incorporated into escapement estimates (Hilborn et al. 1999; Su et al. 2001; Korman et al. 2002).

Sources of uncertainty in escapement estimates vary with estimation method; however, all methods require that assumptions be made about (*i*) observer efficiency and (*ii*) the shape of the curve describing daily fish abundance in the survey area, which is itself dependent on arrival timing and survey life (English et al. 1992; Irvine et al. 1992; Bue et al. 1998). Unfortunately, observer efficiency, arrival timing, and survey life can be highly variable both among years and among streams within a given year. Factors influencing observer efficiency include observer experience, weather conditions, fish behaviour, and physical stream characteristics (Bevan 1961; Shardlow et al. 1987; Jones et al. 1998), while factors influencing survey life include individual body size, spawning density, arrival timing, and physical stream characteristics (Neilson and Geen 1981; Van den Berghe and Gross 1986; Fukushima and Smoker 1997). Arrival timing has a strong heritable genetic component (Smoker et al. 1998; Hodgson and Quinn 2002; Stewart et al. 2002); however, it can also vary among years and streams because of environmental conditions during migration, such as flow and temperature (Hodgson and Quinn 2002; Keefer et al. 2004).

Although the above uncertainties are relevant to escapement monitoring of all Pacific salmon species, we have chosen to focus on coho salmon (*Oncorhynchus kisutch*) populations in our study. Visual surveys of coho salmon populations are especially problematic because of high variability in both observer efficiency and daily abundance patterns. Coho salmon can be difficult to detect because of their colouration and their naturally low spawning abundances, and observer efficiency can be highly variable among surveys (e.g., Hetrick and Nemeth 2003). In addition, several observational studies suggest that the influence of environmental factors on arrival timing is particularly important for coho salmon populations, which frequently display pulsed and bimodal abundance curves and often enter spawning streams during periods of increased flow (Fraser et al. 1983; Holtby et al. 1984; Sandercock 1991).

We developed a Monte Carlo simulation procedure to evaluate the ability of four estimation methods (peak count, T-AUC, L-AUC with a beta-distributed arrival timing model, and an alternative mean count method) to detect 30% declines in coho salmon escapement over 10 years, which is one of several quantitative benchmarks that would warrant listing a coho population as threatened under the listing criteria used by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC). The specific objectives of our study were threefold: (*i*) to compare the ability of the alternative estimation methods to correctly detect declines in coho salmon escapement, (*ii*) to examine the effect of survey frequency (i.e., the number of surveys per year) on the ability to detect trends, and (*iii*) to test the sensitivity of our results to a wide range of scenarios about "true" population parameters and survey designs.

The usefulness of employing a simulation modelling approach to evaluate visual survey designs and estimation methods has been demonstrated for monitoring programs for migratory birds (Thomas 1996) and marine mammals (Adkison et al. 2003). To the best of our knowledge, however, our study of coho salmon visual programs is the first to use simulation modelling to examine how survey design and interannual variability in daily abundance patterns affect the accuracy and precision of trend detection for alternative escapement estimation methods.

## Materials and methods

We developed a Monte Carlo simulation procedure consisting of four major components: (*i*) a model of true coho population dynamics, including annual escapement and daily abundance dynamics in a hypothetical survey area, (*ii*) a visual survey model to generate survey count data with observation error, (*iii*) calculation of alternative visual survey indices from those simulated survey count data using four different estimation methods, and (*iv*) evaluation of monitoring performance for each visual survey estimation method. To generate realistic count data for coho visual surveys, we used existing data sets to estimate interannual variability in daily abundance patterns and between-survey variability in observer efficiency. In the first half of our Methods section, we describe the data sets and analyses used to parameterize daily abundance dynamics and observer efficiency, while in the second half of the section we describe the simulation procedure. Model parameters are denoted using italicized lowercase letters (e.g., $m$), state variables are denoted using italicized uppercase letters (e.g., $A$), and functions are denoted using bold uppercase letters (e.g., **F**).

### Data analysis

#### *Daily abundance patterns*

We used 33 existing coho salmon visual foot survey data sets provided by Fisheries and Oceans Canada (DFO) stock assessment personnel to select an appropriate model to describe daily abundance patterns (referred to as daily abun-

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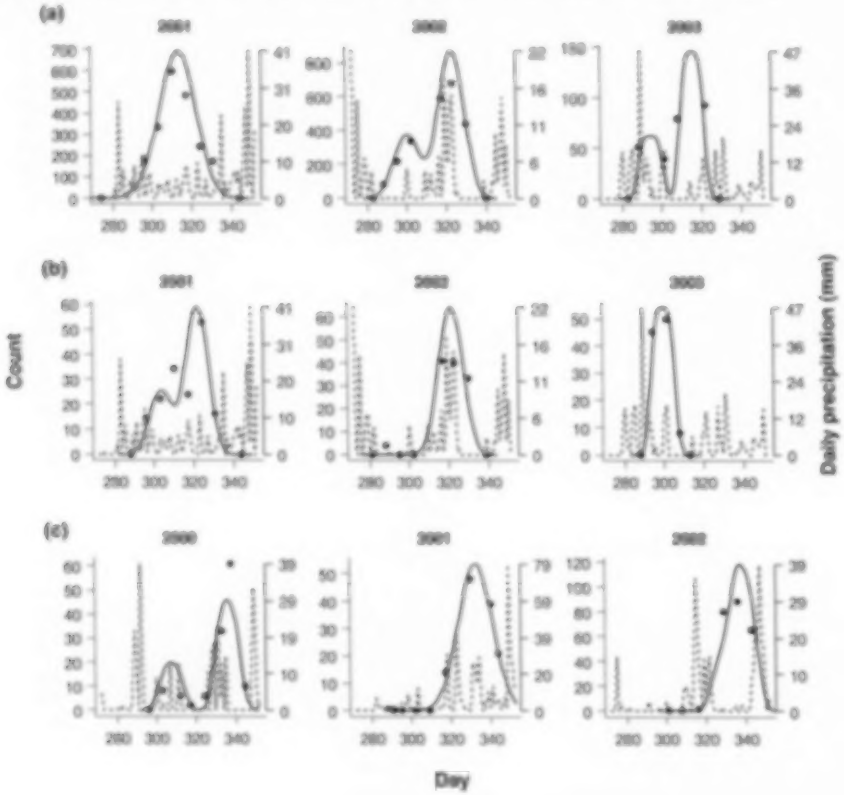
**Fig. 1.** Daily precipitation levels (broken lines) plus observed (solid circles) and predicted (solid lines) spawner abundances from visual survey counts for coho salmon (*Oncorhynchus kisutch*) visual survey data sets from (*a*) Blue River and (*b*) Cook Creek in the North Thompson Watershed, British Columbia, and from (*c*) Bonnell Creek on Vancouver Island, British Columbia.




dance model) and estimate interannual variability in model parameter values (e.g., Fig. 1, Appendix A). Data sets were collected from 11 streams over a period of 3 years. Nine of the streams were tributaries to the North Thompson River in the Fraser River system, British Columbia (BC; data provided by R. Bailey, DFO, BC Interior Region Stock Assessment, 985 McGill Place, Kamloops, BC V2C 6X6, personal communication), and the other two streams were located on the east coast of Vancouver Island, BC (data provided by K. Simpson, DFO, BC South Coast Stock Assessment, 3225 Stephenson Point Road, Nanaimo, BC V9T 1K3, personal communication). All data sets had a minimum of five survey counts per year. Based on the results of model selection analysis, we selected a mixture model that was able to generate both unimodal and bimodal abundance curves (Appendix A). The selected mixture model required four parameters to be estimated from visual survey data sets ($m$, $k$, $\sigma^{*1}$, and $\sigma^{*2}$ in Table 1 and Appendix A). While the use of the mixture model may seem unwarranted given the small number of data points and the possibility of over-fitting, its use is justified by the high interannual variability in coho abundance curves arising from infrequent precipitation events (Fig. 1). It is apparent that coho salmon are more likely to enter streams during or immediately after several days of high-intensity precipitation and that bimodal abundance curves are common in years when dry periods are interspersed with periods of high precipitation. This level of variability cannot be produced using simpler models that restrict daily abundance dynamics to a single mode.

Among-year variation for each of the four mixture model parameters was calculated assuming that each stream $i$ had a set of stream-specific mean parameter values from which daily abundance patterns deviated each year. For a given mixture model parameter $\theta$, the actual parameter value observed for stream $i$ in year $t$ was a function of the stream-specific mean $\bar{\theta}_i$ and a stock- and year-specific deviation $\varepsilon_{i,t}$, e.g.,

$$\theta_{i,t} = \bar{\theta}_i + \varepsilon_{i,t} \quad (1)$$

Mean parameter values reflect effects of stream-specific factors influencing arrival timing, such as local adaptation and migration distance (e.g., Smoker et al. 1998; Hodgson and Quinn 2002; Keefer et al. 2004). The methods used to estimate $\varepsilon_{i,t}$ for each of the four mixture model parameters are described in Appendix A.

### *Observer efficiency*

Data on observer efficiency for adult coho salmon foot surveys were obtained from previous studies conducted on Black Creek, Vancouver Island, BC (J. Irvine, DFO, 3190 Hammond Bay Road, Nanaimo, BC V9T 6N7, unpublished data). The study design, in which observers visually inspected

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**Table 1.** Simulation parameters for the baseline scenario.

| Parameter | Value | Description |
|---|---|---|
| **True population parameters** | | |
| $E_0$ | 500 | Initial escapement in year 0 |
| Decline | 40%** | Percent decline in escapement over 10 years |
| $r$ | –0.057** | Annual rate of population growth associated with decline |
| $m$ | 301.8 | Stream-specific mean date of arrival (annual days) |
| $k$ | 12.4 | Stream-specific distance parameter |
| $\sigma^{*1}$ | 4.7 | Stream-specific standard deviation of arrival timing for first curve in mixture model |
| $\sigma^{*2}$ | 5.7 | Stream-specific standard deviation of arrival timing for second curve in mixture model |
| $\tau_m$ | 7.1** | Standard deviation of year-specific random effect for $m$ |
| $\tau_k$ | 8.1** | Standard deviation of year-specific random effect for $k$ |
| $\tau_{\sigma_1}$ | 2.3** | Standard deviation of year-specific random effect for $\sigma^{*1}$ |
| $\tau_{\sigma_2}$ | 3.0** | Standard deviation of year-specific random effect for $\sigma^{*2}$ |
| $s$ | 12.8 | Survey life for fish arriving on the median arrival date |
| $z$ | 0.3 | Proportion parameter for the mixture run timing model |
| $v$ | 0.865** | Average true observer efficiency |
| **Survey parameters** | | |
| $f_{max}$ | (1, 2, 3,…,8)** | Number of surveys per year |
| $\hat{v}$ | 0.865 | Estimated observer efficiency |
| CV($\hat{s}$) | 0.2** | Coefficient of variation of survey life estimate |
| $\mu_s$ | 12.8 | Mean of prior distribution on $s$ |
| **Trend detection parameters** | | |
| Decline* | 30% | Critical percent decline in escapement over 10 years |
| $r^*$ | –0.04 | Critical annual rate of population growth associated with decline* |

**Note:** The symbol ** indicates that sensitivity analyses were conducted on the parameter value (see Table 2). A detailed description of the mixture model used to describe daily abundance dynamics is given in Appendix A.

fenced off segments of stream prior to electrofishing, was repeated for 50 surveys occurring over 7 years. A more detailed description of the study design and an analysis of the first 3 years of data are available in Irvine et al. (1992). Analysis of the Black Creek observer efficiency data showed that the relationship between true abundance estimated from electrofishing, $N$, and survey counts, $C$, was linear, and that the intercept of the linear best-fit line did not differ significantly from zero ($C = a + bN$; null hypothesis ($H_0$): $a = 0$; $p = 0.412$, $R^2 = 0.92$). There was no significant difference in the slope of the regression among years (analysis of covariance; $F = 2.09$, $p = 0.155$). We therefore estimated the average observer efficiency over all surveys as the slope of the zero-intercept linear regression between $N$ and $C$. The estimated slope was 0.865 ($R^2 = 0.95$; standard error = 0.03), indicating that on average, 86.5% of fish were detected.

## Simulation procedure

We first created a baseline scenario to be used in the simulation procedure, which, based on our analyses, provided the most realistic representation of population and survey dynamics. Parameter values used in the baseline scenario were the maximum likelihood estimates obtained from fitting the daily abundance and observation models described in the previous two sections to empirical data (a summary of parameter values used in the baseline scenario is provided in Table 1). We then used sensitivity analyses to examine how deviations from parameter values used in the baseline scenario affected the performance of each estimation method. The basic steps in the simulation procedure are as follows: (*i*) Generate a true 10-year escapement time series with a rate of decline (40% decline) greater than the critical rate of decline that would result in a population being assessed as threatened under COSEWIC listing criteria (30% decline). (*ii*) Generate true daily abundances with random variation for each year $t$ in the escapement time series. (*iii*) Generate count data with observation error for each survey frequency considered ($f_{max}$ = 1,2,…,8 surveys per year) within year $t$. (*iv*) Calculate an estimated index of escapement for year $t$ for each of the four estimation methods using the count data from $f_{max}$ surveys. (*v*) Using the 10 years of observed index values, calculate probability associated with $H_0$: stock is not threatened. (*vi*) If the probability of $H_0$ is less than a prespecified confidence level (20%), reject $H_0$ and designate stock as threatened. (*vii*) Repeat steps (*i*) to (*vi*) for 1000 simulation trials. (*viii*) Calculate the probability of detecting a threatened population as the proportion of trials that correctly assess stock status as threatened for each combination of estimation method and survey frequency considered.

### *Annual escapement trends*

We used an exponential growth model to generate a declining time series of true escapement values

$$E_t = E_0 e^{rt} \quad (2)$$

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where $E$ is true escapement, $t$ is time in years, and $r$ is the intrinsic rate of population growth (i.e., for a declining population, $r < 0$). For the baseline scenario, in which the true percent decline in escapement was 40% over 10 years, the value of $r$ was –0.057. In comparison, the critical COSEWIC rate of decline used to designate a population as threatened is a 30% decline over 10 years ($r^* = -0.04$).

***Daily abundance dynamics***

The mixture model used to estimate among-year variability in daily abundance patterns was used to simulate true daily abundances for each year $t$ in the escapement time series (Appendix A). The total duration of simulated fish presence in the survey area ranged from 17 to 91 days (mean = 51.5 days, $n = 1000$), which was realistic compared with the range of 19 to 82 days (mean = 47.3 days, $n = 33$) observed for the visual survey data sets used to parameterize daily abundance models. Interannual variability in daily abundance patterns was incorporated into simulated true data using the following variation of eq. 1 to describe a given abundance model parameter $\theta$:

$$\theta_{t,\gamma} = \bar{\theta}_t + \Upsilon_\gamma \quad (3)$$

where $\Upsilon_\gamma$ is a year-specific random effect. For each parameter $\theta$, $\Upsilon$ was assumed to be a normally distributed random variable with a mean of zero and standard deviation of $\tau$:

$$\Upsilon = \mathbf{N}(0,\tau) \quad (4)$$

where the value of $\tau$ was specific to each parameter (denoted as $\tau_\mu$, $\tau_\lambda$, $\tau_{\sigma_1}$, and $\tau_{\sigma_2}$ in Table 1). In the baseline scenario, values of $\tau$ were set equal to the mean values estimated from visual survey data sets (see Appendix A for description).

***Visual survey model***

The mean count, T-AUC, and L-AUC methods required a minimum of two, three, and five surveys per year, respectively. Survey dates were selected based on the assumption that observers would have some knowledge of historic daily abundance curves within a study stream. On average, survey dates were centred on the historic peak day of spawning abundance for the stream, $d_{PK}$. We developed a simple algorithm in which survey events were clustered near $d_{PK}$ when survey frequency was low. The single survey for the one-survey case of the peak count method was conducted on $d_{PK}$, while the surveys for the two-survey case were conducted 1 week before and 1 week after $d_{PK}$. For the three- to eight-survey cases, the total number of days over which counts were conducted ($l$) was dependent on survey frequency ($f_{max}$) as follows:

$$l = \begin{cases} 42 \text{ days} & f_{max} = 3 \\ 56 \text{ days} & f_{max} = 4 \\ 70 \text{ days} & f_{max} = 5 \\ 84 \text{ days} & f_{max} \geq 6 \end{cases} \quad (5)$$

The first survey date was randomly selected from a 7-day period that occurred $0.5l$ days before $d_{PK}$ using a uniform distribution, and subsequent surveys were evenly spaced over the next $l$ days. Simulated survey counts were generated randomly from a Poisson distribution with a rate parameter $\lambda = vN_d$, where $v$ is the average observer efficiency estimated from Black Creek observer efficiency studies (above).

***Alternative escapement index methods***

The maximum count value over surveys conducted in a given year was used as an index of annual escapement for the peak count method:

$$I_{PK} = \max(C_1, C_2, \ldots, C_{f_{max}}) \quad (6)$$

while the mean of count values was used as an index of annual escapement for the mean count method:

$$I_{MN} = \frac{1}{f_{max}} \sum_{d=1}^{d=f_{max}} C_d \quad (7)$$

The T-AUC method employs a simple trapezoidal approximation to calculate the area under the observed abundance curve for each year:

$$\text{AUC} = \sum_{d=2}^{f_{max}+1} (u_d - u_{d-1}) \frac{(C_d + C_{d-1})}{2} \quad (8)$$

where $u_d$ is the day on which the $d$th survey was conducted. We used Bue et al.'s (1998) approximation:

$$\text{AUC}_{first} = \frac{C_1 \hat{s}_t}{2} \quad (9)$$

$$\text{AUC}_{last} = \frac{C_{last} \hat{s}_t}{2} \quad (10)$$

where $\hat{s}_t$ is an estimate of survey life for year $t$. When year- and stream-specific estimates of survey life are not available, as would be expected for extensive survey programs, survey life estimates must be extrapolated between years and (or) streams. In the baseline scenario, we model a monitoring program in which a year-specific survey life value is estimated for a single stream and then applied to multiple streams within that year. An escapement estimate is derived from eq. 8 as

$$\hat{E} = \frac{\text{AUC}}{\hat{s}_t \hat{v}} \quad (11)$$

where $\hat{v}$ is an estimate of average observer efficiency. The selection of $\hat{v}$ and $\hat{s}_t$ values for each simulation trial was based on the assumption that stock assessment analysts had some knowledge of the true underlying parameter distributions, which is reasonable given the numerous studies that have been conducted on these parameters. The value of $\hat{v}$ was held constant at 0.865, which was the average observer efficiency value used to generate true count data. Observation error in $\hat{s}_t$ was incorporated into the simulation procedure by assuming that $\hat{s}_t$ was a random normal variable with a mean, $\mu_{\hat{s}_t}$, equal to $s$ and a coefficient of variation, CV($\hat{s}$), of 0.2. While the selection of CV($\hat{s}$) = 0.2 for survey life estimates in the baseline scenario was somewhat arbitrary, studies of the length of time coho salmon spend on their redds (redd residence time) in two coastal streams suggest that this value is reasonable for monitoring programs that estimate survey life for a single stream each year and then extrapolate that value to other streams. Over a period of 4 years, the redd residence time estimates for French Creek

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and Black Creek on eastern Vancouver Island, BC, differed from each other by an average of 4.5 days (range of difference = 0.5–8.7 days; English et al. 1992; Irvine et al. 1992).

The L-AUC method (Hilborn et al. 1999) estimates escapement by treating it as an unknown parameter in a maximum likelihood estimation (MLE) procedure. The L-AUC method consists of three components. First, a daily abundance model is used to predict daily fish abundance in the survey area, $\hat{N}_d$. We used a beta distribution model to describe daily abundance dynamics in the L-AUC method (Appendix A). Second, an observation model is used to predict the number of fish counted, $\hat{C}_d$, as a function of $\hat{N}_d$ and an estimate of observer efficiency $\hat{v}$

$$\hat{C}_d = \hat{v}\hat{N}_d \quad (12)$$

Third, a statistical model with a goodness of fit criterion measures the agreement between predicted and observed count values. For this last component, MLE was used to fit predicted counts from eq. 12 to observed counts by estimating total escapement ($\hat{E}$), survey life ($\hat{s}$), and the two shape parameters of the beta distribution ($\hat{\alpha}$ and $\hat{\beta}$). These four parameters were estimated using a penalized likelihood function that assumed a Poisson error distribution for the count data (eq. A3 in Appendix A) and a normal prior distribution on the parameter $s$, with a mean of $\mu_s$ and a standard deviation of $\sigma_s$. The total negative log-likelihood was thus

$$\ell(C_1, C_2, \ldots, C_{f_{max}} | v, \alpha, \beta, s) = \frac{(s-\mu_s)^2}{2\sigma_s^2} + \sum_{d=1}^{d=f_{max}} \hat{C}_d(v, \alpha, \beta, s) - C_d \log[\hat{C}_d(v, \alpha, \beta, s)] \quad (13)$$

where $C_d$ and $\hat{C}_d$ are the observed and predicted count values, respectively, for day $d$. The L-AUC method was only applicable to survey frequencies of five per year or greater to prevent model overparameterization. The value of $\mu_s$ was set equal to the true value of $s$ used to generate the data, and the value of $\hat{v}$ was held constant at 0.865. Including a prior distribution on $s$ was necessary to ensure parameter stability in the estimation procedure. In some cases, $v$ can be treated as a free parameter in the MLE procedure (Hilborn et al. 1999); however, parameter estimates of $\alpha$, $\beta$, and $s$ were highly correlated at all survey frequencies examined when $v$ was estimated rather than assumed.

### *Evaluation of monitoring performance*

An observed escapement index, $I_t$ ($t = 1,2,\ldots,10$), was generated for each combination of estimation method and survey frequency considered (hereafter referred to as monitoring designs). We used a simple linear regression of log-transformed index data on year, i.e.,

$$\log_e(I_t) = \log_e(\hat{I}_0) + \hat{r}t \quad (14)$$

to estimate the rate of population growth $\hat{r}$. A one-tailed $t$ test was used to designate population status as threatened using the COSEWIC assessment criteria of $r \leq -0.04$ over 10 years ($H_0$ (decline < 30%): $r > -0.04$; $H_1$ (decline ≥30%): $r \leq -0.04$). We placed equal weight on the type I and type II error probabilities for detecting significant declines in escapement ($\alpha = \beta = 0.2$). Thus, $H_0$ was rejected and the population was assessed as threatened when $p \leq 0.2$ for the $t$ test. Because the true $r$ value used to generate annual escapement followed $H_1$, trend detection was considered successful when this null hypothesis was rejected. The entire simulation procedure was repeated for 1000 Monte Carlo trials, and monitoring performance was measured by the following three criteria: (*i*) the proportion of trials in which a threatened population was correctly detected; (*ii*) the minimum number of years required to correctly detect a threatened population in at least 80% of Monte Carlo trials, and (*iii*) how the probability of detecting a threatened population changed in response to different levels of true population decline. For this final criterion, we examined a range of alternative rates of decline (0%, 2%, 4%,…,60%) over 10 years by changing the true value of $r$ in eq. 2.

### *Sensitivity analysis*

We used sensitivity analyses to examine how deviations from assumptions about interannual variability in daily abundance patterns and among-survey variability in observer efficiency affected the probability of detecting a threatened population for each monitoring design. For the first analysis, three additional levels of variability in daily abundance patterns were examined (none, low, and high) by changing the values of $\tau$ in eq. 4. To cover the range of interannual variability observed among the 11 streams analyzed, the value of $\tau$ in the low and high variability scenarios was set equal to the highest and lowest $\tau_i$ values estimated from the 11 streams (Table 2). In the second sensitivity analysis, three alternative levels of variability in observer efficiency were examined (none, low, and high; Table 2). Because the variance of a Poisson distribution is equal to the mean, variability in observer efficiency was altered by changing $v$. For a given level of $N$, the variance of $C$ was increased when $v$ was increased. In the no-variability scenario, the number of fish observed was nonrandom ($C_d = N_d$ for all surveys).

### *Survey design scenarios*

To determine how the design of visual survey monitoring programs could affect the probability of detecting a threatened population, we examined a range of alternative scenarios on (*i*) the level of error in estimates of survey life, CV($\hat{s}$), (*ii*) survey spacing, and (*iii*) variation in survey frequency among years. In the first of these analyses, we examined the sensitivity of T-AUC performance to three alternative scenarios for CV($\hat{s}$) (none, low, high; Table 2). Only the T-AUC method was considered in the analysis because it is the only method that requires an annual estimate of survey life. In comparison, the L-AUC method treats survey life as an unknown parameter that is estimated annually from the count data. We examined how the spacing of survey events within a year affected monitoring performance by considering two alternatives to the baseline scenario shown in eq. 5. In the first of these, surveys were evenly spaced over $l = 77$ days. The second was a random spacing scenario in which the survey period of $l = 77$ days was stratified into $f_{max}$ intervals of even size, and one survey date was randomly sampled from a uniform distribution within each interval. To examine how among-year variation in survey frequency affected monitoring performance, we considered three alternative scenarios. For each scenario, the survey frequency for a given year was

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**Table 2.** Alternative scenarios about true population dynamics and survey design tested in sensitivity analyses and a subset of results for designs with three and six surveys per year.

| Variable (baseline values) | Scenario | Values | Probability of detecting a threatened population for three/six surveys per year: Peak | Mean | T-AUC | L-AUC |
|---|---|---|---|---|---|---|
| Baseline | | | 0.36 / 0.41 | 0.44 / 0.84 | 0.39 / 0.45 | NA / 0.79 |
| **True population parameters** | | | | | | |
| Variability in daily abundances | None | $\tau = (0, 0, 0, 0)$ | 0.87 / 0.75 | 0.85 / 0.92 | 0.44 / 0.44 | NA / 0.94 |
| $\tau = [\tau_w, \tau_4, \tau_{\sigma_1}, \tau_{\sigma_2}]$ | Low | $\tau = (2.5, 1.4, 2.6, 2.9)$ | 0.41 / 0.47 | 0.55 / 0.91 | 0.39 / 0.43 | NA / 0.92 |
| $= (6.7, 5.6, 2.9, 2.4)$ | High | $\tau = (9.4, 8.9, 4.0, 1.0)$ | 0.30 / 0.34 | 0.28 / 0.55 | 0.27 / 0.38 | NA / 0.38 |
| Variability in observer efficiency | None | See text | 0.35 / 0.41 | 0.48 / 0.95 | 0.38 / 0.44 | NA / 0.89 |
| ($v = 0.86$) | Low | $v = 0.76$ | 0.35 / 0.41 | 0.46 / 0.81 | 0.39 / 0.46 | NA / 0.78 |
| | High | $v = 0.96$ | 0.36 / 0.41 | 0.44 / 0.74 | 0.37 / 0.42 | NA / 0.71 |
| **Survey designs** | | | | | | |
| Error in survey life estimate | None | $CV(\hat{s}) = 0$ | NA | NA | 0.65 / 0.96 | NA |
| ($CV(\hat{s}) = 0.2$) | Low | $CV(\hat{s}) = 0.1$ | NA | NA | 0.54 / 0.66 | NA |
| | High | $CV(\hat{s}) = 0.3$ | NA | NA | 0.33 / 0.33 | NA |
| Survey spacing | Even | See text | 0.28 / 0.39 | 0.26 / 0.83 | 0.28 / 0.43 | NA / 0.80 |
| | Random | See text | 0.27 / 0.36 | 0.28 / 0.51 | 0.28 / 0.40 | NA / 0.55 |
| Variation in survey frequency | High | $f_{max} = U(3, 8)$ | 0.38 | 0.55 | 0.42 | NA |
| | Medium | $f_{max} = U(4, 7)$ | 0.39 | 0.59 | 0.42 | NA |
| | Low | $f_{max} = U(5, 6)$ | 0.39 | 0.73 | 0.43 | 0.68 |

**Note:** The function $U(g, h)$ denotes a uniform random number with lower bound $g$ and upper bound $h$. T-AUC, trapezoidal area-under-the-curve method; L-AUC, likelihood approach to area-under-the-curve escapement estimation.

selected from a random uniform distribution (Table 2). Because of the requirement for a minimum of five surveys per year for the L-AUC method, only one of the three alternative scenarios (low variability) was applicable.

## Results

### Baseline scenario

In the baseline scenario, which, based on our analysis, provided the closest representation of survey dynamics for a population experiencing a 40% decline in escapement over 10 years, all of the monitoring designs we considered produced relatively unbiased estimates of $r$ when averaged across 1000 simulations (±3%). The probability of detecting a threatened population increased with increasing survey frequency for all four estimation methods; however, the mean count and L-AUC methods were able to achieve greater gains in the probability of detecting a threatened population than other two methods (Fig. 2). The L-AUC method achieved only slightly lower probability than the mean count method at all survey frequencies examined. The rank order of the four estimation methods remained the same as in Fig. 2 when performance was measured by the minimum number of years required to achieve an 80% probability of detecting a threatened population (Table 3); however, only the mean count and L-AUC methods met this criterion within the required 10-year period.

The effect of survey frequency on the probability of detecting a threatened population depended on the true population decline relative to the null hypothesis ($H_0$ (de-

**Fig. 2.** Probability of detecting a threatened population (>30% decline in escapement over 10 years) as a function of survey frequency for mean count (triangles), likelihood approach to area-under-the-curve (L-AUC, diamonds), trapezoidal area-under-the-curve (T-AUC, squares), and peak count (circles) estimation methods in the baseline scenario, in which the actual rate of decline is 40% over 10 years. The mean count, T-AUC, and L-AUC methods require minimum survey frequencies of two, three, and five surveys per year, respectively.

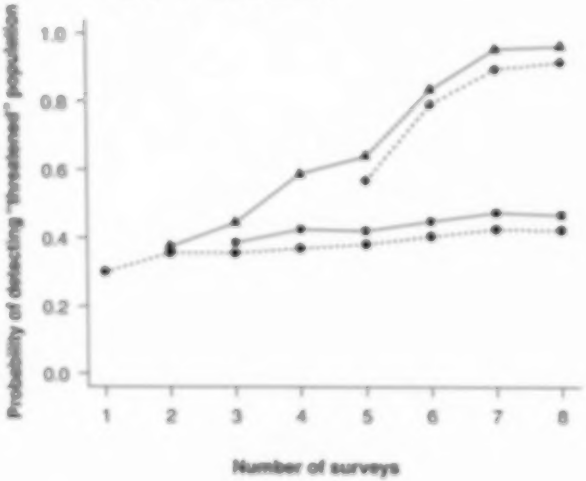


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**Table 3.** Minimum number of years required to achieve 80% probability of detecting a threatened population (decline > 30% over 10 years) in the baseline scenario in which the actual rate of decline is 40% over 10 years.

| | Survey frequency | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 |
| Peak | >20 | >20 | >20 | >20 | >20 | >20 | 20 | 20 |
| Mean | — | >20 | 19 | 15 | 13 | 10 | 8 | 8 |
| T-AUC | — | — | >20 | >20 | >20 | 19 | 19 | 19 |
| L-AUC | — | — | — | — | 15 | 10 | 9 | 8 |

**Note:** T-AUC, trapezoidal area-under-the-curve method; L-AUC, likelihood approach to area-under-the-curve escapement estimation.

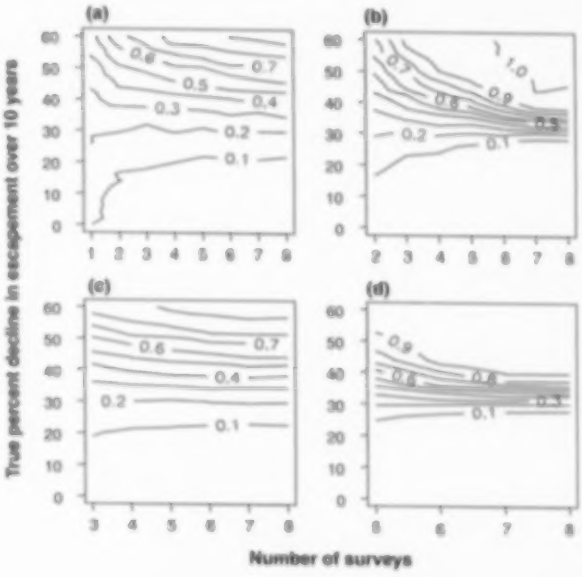
cline ≤ 30%): $r \geq -0.04$) used in trend detection analysis (Fig. 3). When $H_0$ was actually wrong and population declines were large (i.e., decline > 30%; $r \leq -0.04$), the probability of detecting a threatened population increased with increasing survey frequency for all four estimation methods. Conversely, when $H_0$ was true and population declines were small or nonexistent (i.e., decline ≤ 30%; $r > -0.04$), the probability of detecting a threatened population decreased with increasing survey frequency. We use the term responsive to describe a monitoring program in which the probability of detecting a threatened population changes quickly in response to changes in the actual percent decline. The mean count and L-AUC methods became increasingly responsive to changes in the true percent decline as survey frequency increased (as shown by the narrowing of contour lines in Fig. 3). The high responsiveness of the mean count and L-AUC methods increased the probability of correctly assessing a population as threatened when it really was threatened and reduced the probability of incorrectly assessing a population as threatened when it was not. As an example of the latter case, when the true percent decline was only 20% over 10 years (i.e., not threatened), the mean count method had a less than 10% probability of incorrectly assessing the population as threatened at five or more survey counts per year, while the peak count and T-AUC method had greater than 10% probability.

## Sensitivity analysis

The probability of detecting a threatened population was dependent on the level of interannual variability in daily abundance curves ($\tau$ in eq. 4 and Table 2) for all four monitoring methods; however, the mean count method maintained the highest level of performance at all levels of variability examined (Table 2). The peak count method required perfectly consistent daily abundance patterns over all years ($\tau = 0$) to achieve levels of performance comparable with those achieved by the mean count method in the baseline scenario. In contrast, the T-AUC method was unable to achieve greater than a 55% probability of detecting a threatened population, even when daily abundance patterns were held perfectly constant.

The range of among-survey variability in observer efficiency examined, from $v$ known exactly to $v = 0.96$, had a relatively small effect on the probability of detecting a threatened population for all estimation methods (Table 2). Losses in performance associated with increased variability above the baseline scenario and gains in performance associated with decreased variability below the baseline scenario were greater for the mean count and L-AUC methods; however, the deviations remained less than 10% in probability. The mean count method still achieved higher levels of performance than the other three methods at all levels of among-survey variability examined.

**Fig. 3.** Sensitivity of the probability (contour lines) of detecting the rate of decline associated with a threatened population (>30% decline in escapement over 10 years) to the true percent decline in escapement and survey frequency for (*a*) peak count, (*b*) mean count, (*c*) trapezoidal area-under-the-curve (T-AUC), and (*d*) likelihood approach to area-under-the-curve (L-AUC) methods. Note that *x* axes have different scales for each estimation method.




## Survey design scenarios

The performance of the T-AUC method was highly sensitive to the level of error in estimates of survey life (Table 2). Perfect information about survey life, $CV(\hat{s}) = 0$, was needed to obtain the level of performance achieved by the mean count method in the baseline scenario. The probability of detecting a threatened population for all four monitoring methods was dependent on the spacing of survey events within a year, although this was particularly true for the mean count and L-AUC methods (Table 2). For most monitoring designs considered, performance was greatest when surveys were spaced according to the baseline algorithm that increasingly clustered surveys around the historic peak date of spawning abundance when survey frequency was low (eq. 5). The random spacing scenario resulted in the lowest performance for all methods; however, the loss of probability of detecting a threatened population under the random spacing scenario was especially large for the mean count and L-AUC methods.

Examination of alternative scenarios regarding among-year variability in survey frequency revealed that when survey fre-

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quency varied between years, monitoring performance tended to be limited by the lowest survey frequency in the time series (Table 2). While this effect was observed for all estimation methods, it was particularly notable for the mean count and L-AUC methods, which achieved the greatest gains in performance with increased survey frequency. For example, when survey frequency varied between three and five counts per year, the probability of detecting a threatened population for each method was similar to that achieved with a constant survey frequency of three. Additionally, when survey frequency varied between three and eight, the level of probability was similar to that achieved with a constant survey frequency of four.

## Discussion

The results of our simulation analysis suggest that a simple mean count method is more suitable than commonly used visual survey estimation methods for monitoring salmon escapement for several reasons (Table 4). While all four methods that we examined estimated the "true" rate of population decline with relatively low bias, the mean count and L-AUC methods consistently achieved higher levels of precision (as reflected by greater probability of detecting a threatened population) than peak count and T-AUC methods over a wide range of scenarios about true population parameters and survey design. High precision is a desirable property for monitoring programs because it increases the probability of correctly estimating the true status of a population. In addition to higher levels of precision, the mean count and T-AUC methods required fewer years to detect the rate of decline associated with a threatened population, which is a desirable property for a monitoring program because it provides an early warning that recovery actions are likely necessary. While escapement monitoring programs should be able to reliably detect situations of concern, such as a rate of population decline that would result in a stock being assessed as threatened under COSEWIC, they should also minimize the probability of falsely detecting these situations. By examining the response of monitoring performance to varying levels of actual population decline, we have shown that the mean count and L-AUC methods perform better than the other two methods using both of these criteria.

The performance of the L-AUC method was comparable with that of the mean count method, which may lead one to conclude that the L-AUC method is more useful for escapement monitoring given that it provides an absolute estimate of escapement instead of only a relative index. The performance of the L-AUC method in our study is likely optimistic, however, because of our treatment of the observer efficiency parameter estimate in the MLE procedure. By treating observer efficiency as a fixed parameter and assuming that the underlying mean parameter value was known without error, we allowed the estimation procedure to underestimate the level of uncertainty in L-AUC escapement estimates. As discussed in the Alternative escapement index methods section of the Materials and methods, this assumption was necessary to prevent model overparameterization. Three additional disadvantages of the L-AUC method are that its estimation procedure is more complicated than that of the mean count method, it requires prior knowledge of stream-specific survey life, and it is limited to survey designs with five or more survey counts per year, which is not always possible for extensive survey programs (D. Peacock, DFO, 202-417 Second Avenue West, Prince Rupert, BC V8J 1G8, personal communication). We therefore conclude that the mean count method is better suited than the L-AUC method for extensive monitoring of coho salmon escapements.

The success of the mean count method can be attributed to its simple, data-based estimation procedure that requires no assumptions to be made about the shape of the daily abundance curve or the length of time fish remain in the survey area. In contrast, both the peak count and T-AUC methods require strong assumptions about at least one of these factors, which limits the monitoring performance of these two methods. For example, the peak count method relies on the assumption that the ratio of the peak count to total escapement is constant among years. Our results show that this assumption is weakly supported for coho salmon stocks. Visual survey data used to parameterize daily abundances showed high interannual variability in both the timing of fish presence and the shape of the observed abundance pattern. In utilizing information from only one survey event each year (i.e., the survey in which the highest count value was obtained), the peak count method fails to incorporate information about the shape of the abundance curve into annual escapement indices. In contrast, the mean count method incorporates all available information on the shape of the abundance curve into the escapement index by using data from all surveys conducted in a year and is thus able to achieve large gains in monitoring performance with increased survey frequency.

The T-AUC method also uses information from all survey events conducted in a year; however, error in survey life estimates limited the gains in monitoring performance associated with increased survey frequency that were observed for the mean count method. Only when error in survey life estimates was low ($CV(\hat{s}) = 0.10$) or absent ($CV(\hat{s}) = 0$) was the performance of the T-AUC method comparable with that of the mean count method in the baseline scenario. Hill (1997) also found that when errors in survey life were relatively low (i.e., survey life treated as a random normal variable with mean = 10 days, standard error = 0.5 days, and $CV(\hat{s}) = 0.13$), the reliability of annual escapement estimates derived using the T-AUC method increased with increasing survey frequency. The lower level of error assumed by Hill (1997), compared with our baseline scenario, was because he simulated a monitoring program that obtained year- and stream-specific estimates of survey life.

The requirement for highly precise estimates of survey life in order for the T-AUC method to achieve high probability of detecting a threatened population is consistent with other research showing that the accuracy of annual T-AUC escapement estimates is highly dependent on both year- and stream-specific estimates of survey life (English et al. 1992; Irvine et al. 1992; Bue et al. 1998). Unfortunately, the cost and effort required to estimate this parameter can be high. Such intensive methods for estimating survey life for Pacific salmon include tagging programs and enumeration fences (English et al. 1992; Bue et al. 1998), capture–recapture studies (Manske and Schwarz 2000), and daily observations

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**Table 4.** Summary of monitoring performance, data requirements, and recommended features for each estimation method.

| Method | Maximum probability to detect $r \leq -0.04$[a] | Absolute or relative escapement estimates | Min. no. of surveys per year | Annual estimates of OE and SL | Measure of uncertainty in estimated escapement | Recommended features |
|---|---|---|---|---|---|---|
| Peak count | 48% | Relative | 1 | Not required | No (unless replicate surveys conducted) | Not suitable for stocks with high interannual variability in daily abundance patterns<br>Maintain a constant number of days between surveys each year<br>Cluster surveys around historical peak date when ≤5 surveys per year conducted |
| Mean count | 96% | Relative | 2 | Not required | No (unless replicate surveys conducted) | Maintain a constant number of days between surveys each year<br>Cluster surveys around historical peak date when ≤5 surveys per year conducted |
| T-AUC | 52% | Absolute | 3 | Required | No (unless replicate surveys conducted) | Use year- and stream-specific estimates of SL and OE<br>Maintain a constant number of days between surveys each year<br>Cluster surveys around historical peak date when ≤5 surveys per year conducted |
| L-AUC | 92% | Absolute | 5 (or more) | Depends on number of surveys used | Yes (but dependent on prior information about OE and SL) | Use estimates of SL for prior information<br>Use stream- and year-specific estimates of OE<br>Maintain a constant number of days between surveys each year<br>Cluster surveys around historical peak date when 5 surveys per year conducted |

**Note:** T-AUC, trapezoidal area-under-the-curve method; L-AUC, likelihood approach to area-under-the-curve escapement estimation; OE, observer efficiency; SL, survey life.
[a]At eight survey counts per year when the true $r = -0.057$ over 10 years.

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(Van den Berghe and Gross 1986). There are two ways in which survey life estimates can be extrapolated between years and streams when year- and stream-specific estimates of survey life are not available (Perrin and Irvine 1990). The first approach is the one assumed in the baseline scenario, in which a year-specific survey life value is estimated for a single stream and then applied to multiple streams within that year. The second approach is to apply a constant survey life estimate to all years in a time series. While the second approach of a constant survey life would reduce the accuracy of annual escapement estimates by ignoring interannual variability in survey life, the high levels of monitoring performance achieved by the T-AUC method when survey life was held constant shows that this approach provides a more reliable index of escapement than the first approach. In this case, however, the T-AUC method would serve as only a relative index of escapement, providing the same level of information as the mean count method.

The low sensitivity of monitoring performance for all estimation methods to among-survey variability in observer efficiency is likely a result of the small differences in variability among the four scenarios. For each scenario, we assumed that observation error followed a Poisson distribution with a constant rate parameter set at the mean observer efficiency value estimated from Black Creek observer efficiency studies (Irvine et al. 1992). While varying the mean observer efficiency between different scenarios allowed us to affect the variance of the Poisson distribution, the overall change in the coefficient of variation decreased as daily abundances increased. The assumption of a Poisson error distribution for generating count data is highly uncertain. Unfortunately, the limited data available on among-survey variability for coho salmon and the challenge of separating observation errors from process errors when calculating observer efficiency made it necessary for us to assume an error structure. A Poisson distribution was used because it is commonly associated with count data (Hilborn and Mangel 1997). Korman et al. (2002) also assumed Poisson-distributed observation errors for visual surveys of steelhead (sea-run rainbow trout, *Oncorhynchus mykiss*).

It should be noted that while we did not find a significant difference in mean observer efficiency values among the 7 years of data available for Black Creek coho, this will not necessarily be the case for all species and all streams. In some cases, observer efficiency can vary substantially among years within a single stream (e.g., Bue et al. 1998 for pink salmon, *Oncorhynchus gorbuscha*). The presence of jacks (males that return to spawn after only one summer at sea) in some coho populations could also affect among-survey variability in observer efficiency if the ratio of jack to adult salmon in a stream varies among years, which is common for some coho populations (Sandercock 1991), and if jack salmon are harder to observe, as noted by Irvine et al. (1992). We included only counts of adult salmon in our analysis of observer efficiency. For the above reasons, we recommend that observer efficiency studies be conducted independently on all streams where visual survey methods are used to gain a better understanding of among-survey variability for each stream.

Our evaluation of alternative survey design scenarios regarding the spacing of surveys within a year and variability in survey frequency across years demonstrates the importance of establishing a standardized sampling protocol that can be applied consistently over multiple years. In order for the mean count method to achieve the high levels of monitoring performance seen in the baseline scenario, both the spacing of surveys and the frequency of surveys should remain constant among years. The simple algorithm for spacing surveys used in the baseline scenario (eq. 5), in which survey dates were increasingly clustered around the historical peak date of spawning abundance at low survey frequencies (three–five surveys per year), tended to produce higher levels of monitoring performance at these frequencies than when surveys were spaced evenly over the historic spawning period. While the particular spacing design that maximizes the probability of detecting a threatened population would likely differ between streams because of varying lengths of fish presence, the advantage of clustering surveys near the historic peak date of spawning abundance is expected to apply to all streams. The decreased levels of monitoring performance for the mean count method when survey dates were spaced randomly shows that in order for this method to maximize performance, the number of days between surveys should be held constant among years. These results have implications not only for the design of visual survey programs, but also for the application of these methods to historic time series of count data that have not followed a consistent sampling protocol. When inconsistencies in survey spacing and frequency exist within a time series, the gains in monitoring performance achieved by the mean count method compared with the other methods will be reduced.

The levels of monitoring performance achieved in our simulation study are higher than would be expected in the field because our true population model did not allow for temporal variability in annual escapement trends. Escapement declined deterministically over 10 years for our true population with a constant rate of decline each year. In reality, however, annual trends in salmon escapement can vary greatly among years because of variable fishing mortality and survival rates. While incorporating temporal variability into the escapement model would be expected to decrease the probability of detecting a threatened population, the performance of the four methods relative to each other would remain unchanged.

Although our evaluation of visual survey methods focussed on coho salmon populations, our findings are relevant to the design of extensive survey programs for many salmonid species including pink salmon (Bue et al. 1998), Chinook salmon (*Oncorhynchus tshawytscha*; Parken et al. 2003), and steelhead (Korman et al. 2002). Additional research is needed to determine whether the mean count method is suitable for these species. The simulation modelling approach we used could be easily adapted for other species by reparameterizing the models used to generate daily abundance and survey dynamics. We suggest, however, that the mean count method has the potential to outperform peak count and AUC methods for other salmon species based on the superior performance of the mean count method across a wide range of sensitivity analyses.

In this study, we focused on the ability of visual survey methods to detect changes in escapement within a single spawning stream. However, given that the primary purpose of extensive visual survey programs, as identified in the WSP, is

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to examine distribution and consistency in escapement trends, a useful extension of our simulation framework would be to expand the current single-stock model to a multistock model. The development of a multistock model, in which a subset of populations with co-varying escapement and daily abundance dynamics are randomly selected for monitoring, would allow for explicit consideration of the effects of different spatial and temporal allocations of survey effort on the strength of trend detection within a CU. For example, the question of "what is the optimal allocation of effort between the number of streams monitored and the frequency applied to each stream?" could be examined for individual CUs. This type of information would be useful for the development of WSP monitoring plans aimed at maximizing the strength of trend detection while minimizing survey costs. Future research is needed to develop a means of combining data from several streams into a single performance measure.

While the level of effort afforded to visual survey programs will depend on trade-offs made between program costs and the level of detail required to assess status of fish populations relative to management and conservation goals, applying a mean count method and maintaining constant survey dates among years will maximize the strength of trend detection for a given level of effort. Despite high interannual variability in coho daily abundance dynamics and variable observer efficiency, the mean count method provides higher confidence in trend detection than peak count and T-AUC methods across a wide range of scenarios about true population dynamics and survey design. The peak count method required consistent daily escapement patterns among years to achieve the level of monitoring performance seen for the mean count method in the baseline scenario, while the T-AUC method required almost perfect information about annual survey life values to achieve this level. Both of these conditions are unlikely to be met for extensive monitoring programs. The L-AUC method achieved high levels of monitoring performance in our study; however, large data requirements limit the usefulness of this method for coho salmon. The success of the mean count method can be attributed to its simple, data-based estimation procedure that requires no assumptions about the shape of the daily abundance curve or the length of time fish remain in the survey area.

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## Appendix A

### Selection of a daily abundance model

We considered five candidate models for describing daily abundance of coho salmon in spawning streams (a normal model, a beta model, and three mixture models). Equations describing the five models are shown in Table A1, with model notation defined in Table A2. The letter "M" placed before an equation indicates that it is a component of one of the daily abundance models in Table A1. When describing the mixture models, we use a superscript to denote which of the two component models a given parameter or state variable refers to (e.g., $\sigma'^1$ is the standard deviation of arrival for the first model, and $\sigma'^2$ is the standard deviation of arrival for the second model). Two probability density functions are used in the daily abundance models in Table A1. The first is the normal cumulative distribution function

$$\text{(A1)}\quad \mathbf{F_N}(d,m,\sigma) = \int_{i=0}^{d} \frac{1}{\sigma\sqrt{2\pi}} \exp\left[-\frac{(i-m)^2}{2\sigma^2}\right] di$$

and the second is the beta cumulative distribution function

**Table A1.** Alternative daily abundance models used in model selection analysis.

**Normal model**

Parameters

(M1) $\hat{\Theta}_{\text{Normal}} = \{m,\sigma,s\}$

Predicted states

(M2) $\hat{A}_d = C_T \mathbf{F_N}(d,m,\sigma)$ where $C_T = \sum_{f=1}^{f_{\max}} C_f$

(M3) $\hat{D}_d = C_T \mathbf{F_N}(d-s,m,\sigma)$

(M4) $\hat{C}_d = \hat{A}_d - \hat{D}_d$

**Beta model**

Parameters

(M5) $\hat{\Theta}_{\text{Beta}} = \{\alpha,\beta,s\}$

Predicted states

(M6) $\hat{A}_d = C_T \mathbf{F_B}\left(\frac{d}{n},\alpha,\beta\right)$

(M7) $\hat{D}_d = \begin{cases} C_T \mathbf{F_B}\left(\frac{d-s}{n},\alpha,\beta\right) & \text{for } d \geq s \\ 0 & \text{for } d < s \end{cases}$

(M4) $\hat{C}_d = \hat{A}_d - \hat{D}_d$

**Mixture model**

Parameters

(M8) $\hat{\Theta}_{\text{Mixture}} = \{m'^1, \sigma'^1, k, \sigma'^2\}$

Predicted states

(M9) $\hat{A}'^1_d = zC_T \mathbf{F_N}(d, m'^1, \sigma'^1)$ $\sigma'^1 \geq 2$

(M10) $\hat{D}'^1_d = zC_T \mathbf{F_N}(d-s, m'^1, \sigma'^1)$

(M11) $\hat{A}'^2_d = (1-z)C_T \mathbf{F_N}(d, m'^1+k, \sigma'^2)$ $k \geq 0$, $\sigma'^2 \geq 2$

(M12) $\hat{D}'^2_d = (1-z)C_T \mathbf{F_N}(d-s, m'^1+k, \sigma'^2)$

(M13) $\hat{C}_d = (\hat{A}'^1_d + \hat{A}'^2_d) - (\hat{D}'^1_d + \hat{D}'^2_d)$

**Note:** The functions $\mathbf{F_N}$ and $\mathbf{F_B}$ are defined in eqs. A1–A2. Symbols are defined in Table A2.

$$\text{(A2)}\quad \mathbf{F_B}(x,\alpha,\beta) = \int_{i=0}^{x} i^{\alpha-1}(1-i)^{\beta-1} di$$

Parameter vectors for each of the daily abundance models are denoted $\hat{\Theta}_{\text{model}}$.

Daily abundance for the normal (eqs. M1–M4) and beta models (eqs. M4–M7) is characterized using cumulative distributions of fish arrival and death (Hilborn et al. 1999) that are scaled by the total number of fish observed over all surveys, $C_T$. Application of the beta model requires that start and end dates for arrival are specified so that day can be scaled between 0 and 1. We assumed that start and end dates coincided with the first and last surveys each year, and $n$ is the number of days between these two dates. Daily abundance for the mixture models (eqs. M8–M13) is characterized as two separate normal models. The standard deviations for both component models ($\sigma'^1$ and $\sigma'^2$) were constrained to be equal to or greater than 2 days during estimation. The number of data points for most streams limited the number of parameters that could be estimated for the mixture models to four (eq. M8), making it necessary to fix the values of $s$ and $z$ in eqs. M9–M12 to ensure parameter stability. The value of $s$ was held constant at the mean of coho survey life

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**Table A2.** Definition of symbols used to describe daily abundance models in Table A1.

| Symbol | Definition |
|---|---|
| **Index variables** | |
| $f$ | Survey index ($f$ = 1, 2, ..., $f_{max}$ surveys) |
| $f_{max}$ | Total number of surveys conducted on a given stream within a year |
| $d$ | Day (from annual calendar; January 1 = day 1) |
| $n$ | Total number of days of fish presence in survey area |
| **Observed data** | |
| $C_d$ | Number of fish counted within a single stream on day $d$ |
| $C_T$ | Total number of fish counted within a single stream over all surveys in a year |
| **Predicted states** | |
| Normal and beta models | |
| $\hat{A}_d$ | Cumulative number of fish arriving by survey day $d$ |
| $\hat{D}_d$ | Cumulative number of fish departing by survey day $d$ |
| $\hat{C}_d$ | Predicted number of fish counted on survey day $d$ |
| Mixture models | |
| $\hat{A}^{*1}_d$ | Cumulative number of fish from first component model arriving by $d$ |
| $\hat{A}^{*2}_d$ | Cumulative number of fish from second component model arriving by $d$ |
| $\hat{D}^{*1}_d$ | Cumulative number of fish from first component model departing by $d$ |
| $\hat{D}^{*2}_d$ | Cumulative number of fish from second component model departing by $d$ |
| **Daily abundance model parameters** | |
| Normal model | |
| $m$ | Mean date of arrival (from annual calendar) |
| $\sigma$ | Standard deviation of arrival date |
| $s$ | Survey life (days) |
| Beta model | |
| $\alpha$ | Beta shape parameter 1 |
| $\beta$ | Beta shape parameter 2 |
| Mixture models | |
| $m^{*1}$ | Mean date of arrival for first component model |
| $k$ | Number of days that the mean date of arrival for second component model is offset from that of the first component model |
| $\sigma^{*1}$ | Standard deviation of arrival for first component model |
| $\sigma^{*2}$ | Standard deviation of arrival for second component model |
| $z$ | Proportion of counted fish belonging to first component model |

estimates obtained from empirical studies (12.8 days; Table A3), while three values of $z$ = {0.3, 0.5, 0.7} produced the alternative mixture models. The mixture models differed from the normal and beta models in that they could display both unimodal and bimodal shapes through adjustment of the $k$ parameter. Small $k$ values tended to create unimodal curves, while large values tended to create bimodal curves.

Candidate models were fitted to count data sets using an MLE procedure assuming the following Poisson negative log-likelihood function for the observed counts

$$\text{(A3)}\quad \ell(C_1, C_2, \ldots, C_{f_{max}} | \hat{\Theta}_{model}) = \sum_{i=1}^{i=f_{max}} [\hat{C}_i - C_i \log(\hat{C}_i)]$$

where the predicted counts $\hat{C}_i$ are functions of the daily abundance model parameters $\hat{\Theta}_{model}$. The five candidate models were ranked using the following small sample version of Akaike's information criterion (AIC) (Burnham and Anderson 2002),

$$\text{(A4)}\quad \text{AIC} = -2\ell^* + 2K + \frac{2K(K+1)}{f_{max} - K - 1}$$

where $\ell^*$ is the maximum log-likelihood value, $K$ is the number of parameters to be estimated and $f_{max}$ is the number of count events. The best model for each data set given the candidate models considered was the one that produced the smallest AIC value.

The results of the AIC test showed that the mixture model with $z$ = 0.3 was the best of the five candidate models for the largest number of data sets (mixture ($z$ = 0.3) was best for 10 out of 33 data sets, compared with 8 out of 33 for mixture ($z$ = 0.7), 7 out of 33 for mixture ($z$ = 0.5), 7 out of 33 for beta, and 1 out of 33 for normal). Based on these results, we selected the mixture model ($z$ = 0.3) to estimate interannual variability in abundance model parameters for the simulation procedure.

### Estimation of interannual variability in daily abundances

Recall from eq. 1 that for each of the each of the four

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**Table A3.** Summary of survey life estimates collected from the literature.

| Stream | Location* | Year | Estimate | Source |
|---|---|---|---|---|
| Spring Creek | OR | 1952 | 11.5 | Perrin and Irvine 1990 |
| Flynn Creek | OR | 1966 | 13.1 | Perrin and Irvine 1990 |
| Oregon streams | OR | 1980 | 11.0 | Perrin and Irvine 1990 |
| Harris Creek | WA | 1980–1983 | 10.0 | Perrin and Irvine 1990 |
| Deer Creek | WA | 1981 | 9.2 | Perrin and Irvine 1990 |
| Eagle River | BC | 1982 | 12.5 | Perrin and Irvine 1990 |
| Salmon River | BC | 1982 | 15.0 | Perrin and Irvine 1990 |
| Adams River | BC | 1982 | 10.0 | Perrin and Irvine 1990 |
| Coldwater River | BC | 1982 | 12.5 | Perrin and Irvine 1990 |
| Keogh River | BC | 1985 | 13.0 | Perrin and Irvine 1990 |
| Little Qualicum | BC | 1986 | 13.3 | Perrin and Irvine 1990 |
| French Creek | BC | 1987 | 13.3 | Irvine et al. 1992 |
| Black Creek | BC | 1987 | 16.6 | Irvine et al. 1992; English et al. 1992 |
| Trent River | BC | 1987 | 7.1 | Perrin and Irvine 1990 |
| French Creek | BC | 1988 | 16.7 | Irvine et al. 1992 |
| Black Creek | BC | 1988 | 8.0 | Irvine et al. 1992; English et al. 1992 |
| Trent River | BC | 1988 | 9.6 | Perrin and Irvine 1990 |
| French Creek | BC | 1989 | 15.5 | Irvine et al. 1992; English et al. 1992 |
| Black Creek | BC | 1989 | 15.0 | Irvine et al. 1992; English et al. 1992 |
| Chase River | BC | 1989 | 16.3 | Manske and Schwarz 2000 |
| French Creek | BC | 1990 | 20.3 | English et al. 1992 |
| Black Creek | BC | 1990 | 15.0 | English et al. 1992 |
| Chase River | BC | 1990 | 10.4 | Manske and Schwarz 2000 |
| All streams, OR | OR | — | 11.3 | Perrin and Irvine 1990 |
| Clear Creek | AK | 1996 | 13.8 | Hetrick and Nemeth 2003 |
| Mean | | | 12.8 | |

*AK, Alaska; BC, British Columbia; OR, Oregon; WA, Washington State.

mixture model parameters, among-year variation was calculated assuming that each stream $i$ had a set of stream-specific mean parameter values ($m'^1$, $k$, $\sigma'^1$, and $\sigma'^2$ in Table A2) from which daily abundance patterns deviated each year

(eq. 1 repeated)

$$\theta_{i,t} = \bar{\theta}_i + \varepsilon_{i,t}$$

where $\theta$ is any one of the four model parameters, $\bar{\theta}_i$ is the stream-specific mean parameter value, $t$ is year, and $\varepsilon_{i,t}$ is a stock- and year-specific deviation. For each of the 33 coho salmon visual survey data sets (11 steams, each with 3 years of data) used to estimate interannual variability in daily abundance patterns, an estimate of $\varepsilon_{i,t}$ was calculated by subtracting $\bar{\theta}_i$ from $\theta_{i,t}$. The standard deviation of $\varepsilon_{i,t}$ within each stream, $\tau_i$, was then calculated using the three estimates of $\varepsilon_{i,t}$ ($t = 1, 2, 3$). The 11 values of $\tau_i$ were used to develop alternative scenarios for the simulation of interannual variability in daily abundance patterns.

### Simulation of true daily abundances

To simulate daily abundances for year $t$, the mixture model was modified slightly so that the cumulative normal distributions presented in eqs. M9–M12 were scaled by total escapement for year $t$, $E_t$, instead of total counts. This modification allowed for predictions of the total number of arrivals and deaths that actually occurred up to a given day $d$, as opposed to the total number of arrivals and deaths counted up to $d$. The difference between cumulative arrivals and cumulative deaths on day $d$ thus determines the total abundance of fish that are alive and in the survey area on that day ($N_d$).

### Application of daily abundance model to L-AUC method

The L-AUC method (Hilborn et al. 1999) estimates escapement by treating it as an estimated parameter in an MLE procedure. Application of the beta arrival timing model to the L-AUC method requires a slight modification from the version presented in eqs. M4–M7. The scalar $C_T$ in eqs. M6–M7 is replaced with a total escapement parameter for year $t$, $E_t$. This modification causes eq. M4 to predict the total number of fish alive in the survey area on day $d$, $\hat{N}_d$.

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# Management inferences from a demographic analysis of sea lamprey (*Petromyzon marinus*) in the Laurentian Great Lakes

**Luis Antonio Vélez-Espino, Robert L. McLaughlin, and Thomas C. Pratt**

**Abstract:** We use matrix models incorporating uncertainty in values of life history traits and density-dependent survival to assess pest management strategies implemented by the Great Lakes Fishery Commission to control nonnative sea lamprey (*Petromyzon marinus*) in the Laurentian Great Lakes. The primary method of sea lamprey control has been treatment of rearing tributaries with chemical lampricides, but release of sterilized males and deployment of migratory barriers and traps are important components of the management plan. Uncertainties in the effectiveness of alternative control remain, however. Our models demonstrated that the management target of reducing lampricide use by 20% while maintaining current levels of control could be achieved if alternative methods are used to suppress current lake-wide fecundity rates by 49%–65%, assuming equal lampricide efficiency on larvae and metamorphosing individuals, or by 42%–55% when lampricide mortality on larvae is assumed to be half of that on metamorphosing individuals. At current levels of lampricide use, reduction to 72%–88% of current fecundity rates is recommended to ensure long-term control of sea lamprey populations in the face of uncertainty in current estimates of population growth rates. New control options targeting additional vital rates, such as survival of the parasitic life stage, could further reduce reliance on lampricides while maintaining effective sea lamprey control.

**Résumé :** Des modèles matriciels qui tiennent compte de l'incertitude dans les taux vitaux et la densité-dépendance nous servent à évaluer les stratégies de gestion mises de l'avant par la Commission des pêcheries des Grands Lacs pour contrôler les grandes lamproies marines (*Petromyzon marinus*) non indigènes dans les Grands Lacs laurentiens. La méthode principale de contrôle des grandes lamproies marines a été le traitement chimique des tributaires d'élevage des lamproies avec des lampricides, bien que la libération de mâles stériles et l'érection de barrières migratoires et de pièges fassent aussi partie intégrante du plan de gestion. Il reste, cependant, des incertitudes concernant l'efficacité des méthodes de contrôle de rechange. Nos modèles démontrent que l'objectif de gestion consistant en une réduction de 20 % de l'utilisation des lampricides, tout en maintenant les niveaux actuels de contrôle, est réalisable à la condition que des méthodes de rechange soient utilisées pour réduire les taux actuels de fécondité de 49 % à 65 % à l'échelle des lacs; on présuppose alors que les lampricides ont une efficacité égale sur les larves et les individus en métamorphose. La réduction de fécondité serait de 42 % à 55 %, si on présuppose que la mortalité due au lampricide chez les larves est la moitié de celle des individus en métamorphose. Aux niveaux présents d'utilisation des lampricides, nous recommandons une réduction des taux de fécondité actuels de 72 % à 88 % pour garantir un contrôle à long terme des populations de grandes lamproies marines, compte tenu de l'incertitude des estimations courantes des taux de croissance des populations. De nouvelles tactiques de contrôle qui ciblent la survie du stade parasite du cycle pourraient réduire encore davantage la dépendance des lampricides, tout en maintenant un contrôle efficace des grandes lamproies marines.

[Traduit par la Rédaction]

## Introduction

The invasion of sea lamprey (*Petromyzon marinus*) into the Laurentian Great Lakes was arguably one of the greatest ecological disasters of the 20th century. The parasitic life stage of sea lamprey feeds on blood and tissue of large fishes, often killing the host (Pearce et al. 1980; Smith and Tibbles 1980). Sea lamprey predation, combined with overfishing and habitat change, caused declines in host species such as lake trout (*Salvelinus namaycush*) and lake whitefish

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(*Coregonus clupeaformis*) and altered food webs in the lakes (Morse et al. 2003; Sullivan et al. 2003). In 1954, the governments of Canada and United States created the Great Lakes Fishery Commission (GLFC), and one of the Commission's principal charges was to control and, if possible, eradicate sea lamprey from the Great Lakes (Christie and Goddard 2003).

The GLFC and its contract agents, Fisheries and Oceans Canada and United States Fish and Wildlife Service, have considered numerous control options since the beginning of the control program (Christie and Goddard 2003). The longest used and most successful method is periodic treatment of streams and rivers where sea lampreys reproduce with the chemical lampricide 3-trifluormethyl-4-nitrophenol (TFM) (Schnick 1972; Meyer and Schnick 1980) or a TFM–niclosamide mixture (Boogaard et al. 2003). Lampricides kill larval lamprey rearing in the streams and rivers before the animals migrate to lakes and become parasitic (Brege et al. 2003). Alternative control methods currently in use include capture, sterilization, and release of male sea lamprey to reduce effective population size (Hanson and Manion 1978, 1980; Twohey et al. 2003) and in-stream barriers and traps that block and facilitate the capture of sea lamprey migrating upstream to spawn (Hunn and Youngs 1980). Each control method targets specific vital rates in the sea lamprey's life cycle. Lampricides reduce the survival of larvae, while male sterilization and upstream barriers and traps reduce reproductive success.

The GLFC's most recent vision statement pledged to maintain current levels of control while reducing lampricide use by 20% over 10 years, in addition to the 30% reduction attained in the previous decade, through increased reliance on alternative methods of control (GLFC 2001). The reduced reliance on lampricides was a response to rising costs and growing public concern about introducing chemicals into the environment. The changes in the management targets and the diversity of control options available reveal two important questions. First, how influential are each of the control methods at suppressing the population growth rate of sea lamprey? Second, what mix of control methods would reduce population growth rate most effectively? Results of earlier studies (e.g., Haeseker et al. 2003; Jones et al. 2003) suggested that alternative methods targeting fecundity rates would have a low control potential relative to lampricides. Alternative controls are expected to achieve only modest reductions in population growth rates because of density-independent variation in reproductive success and mechanisms of density-dependent compensation. However, developing and using models that integrate the entire sea lamprey life cycle, incorporating uncertainty and variability in the different aspects of sea lamprey population dynamics, have been identified as important research needs (Jones 2006).

Perturbation analysis (Caswell 2000) provides a useful and yet unused tool for assessing the effect of different control options on the population growth rates of sea lamprey. This form of demographic analysis evaluates the functional dependence of population growth rate ($\lambda$) on vital rates (fecundity, survival, growth). It further facilitates the identification of vital rates and corresponding life stages sensitive to management actions and the assessment of the magnitude of effects due to uncertainty in parameter estimates. Prospective perturbation analysis entails construction of projection matrices from which $\lambda$ and the relative importance of each vital rate (elasticity) are estimated and used to anticipate the effects of management actions (Caswell 2000). Elements of the matrices incorporate the vital rates for each life cycle stage under the assumption that these rates are identical for all individuals in a given stage (see Lefkovitch 1965). It has been demonstrated theoretically and empirically that variation in population responses generated by differences in vital rates between individuals within a stage (i.e., demographic stochasticity) becomes important only at extremely small population sizes (Caughley 1994; Caughley and Gunn 1996; Morris and Doak 2002).

Matrix models are being used increasingly in conservation biology (e.g., Crouse et al. 1987; Cortés 2002; Wilson 2003) and resource management (e.g., Getz and Height 1989; Hayes 2000), where the emphasis is typically on improving population growth rates. They are also suitable for pest management, where the emphasis is on suppressing population growth rates (Gauthier and Brault 1998). In the latter context, matrix models have been used successfully to quantify the dispersal and speed of invasions (Neubert and Caswell 2000), assess the effectiveness of biocontrol agents (Shea and Kelly 1998; McEvoy and Coombs 1999), and assist management decision-making (Rockwell et al. 1997). We use perturbation analysis of a stage-structured matrix model incorporating uncertainty in life history traits and density-dependent survival as a tool to (*i*) identify how sea lamprey populations are expected to respond to control methods affecting different vital rates, (*ii*) estimate the added suppression in fecundity via existing alternative methods that is needed to maintain the current level of control in the face of reduced reliance on lampricides, (*iii*) estimate the overall level of effort that is advisable when uncertainty in population growth rates is considered, and (*iv*) recommend life stages to target with new alternative controls.

## Materials and methods

Our modeling approach consisted of four steps. First, the life cycle of the sea lamprey in the Great Lakes and relevant life history attributes were characterized to construct a matrix population model incorporating biologically and ecologically meaningful life stages. Second, stage-specific vital rates, the basic parameters of the matrix elements, were estimated. We used available time series of spawner abundances and sex ratio information to customize the vital rates for each Great Lake. Mean values of vital rates were used to conduct a deterministic analysis. Variances of trait values were incorporated to conduct a stochastic analysis. Third, for each lake, elasticities of vital rates were computed to provide an overview of how small perturbations of vital rates were expected to affect population growth rates, and larger, direct perturbations of transition matrices were used to simulate the lake-wide effects of different management scenarios. Lastly, we incorporated density dependence in survival into the models and projected population responses to independent and simultaneous changes in the rates of larval survival expected via lampricide treatments and fecundity expected via alternative controls.

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### Characterization of sea lamprey life history

Sea lamprey ammocoetes (larvae) rear in Great Lakes tributaries for several years before undergoing metamorphosis and migrating into a Great Lake to begin their juvenile parasitic phase. Maturing sea lampreys return to tributaries the following year to reproduce and die. Metamorphosis may occur as early as age 2 (Morkert et al. 1998) and as late as age 18 (Manion and Smith 1978), although ages at metamorphosis of 2–6 years are more commonly accepted (Jones et al. 2003; Youson 2003). The juvenile, parasitic stage commences following metamorphosis and can occur in either spring or autumn (Applegate 1950; Bergstedt and Swink 1995). Maturing individuals initiate their spawning migration into streams in the following spring. Thus, the parasitic stage can last 12 or 20 months. Variation in age at metamorphosis and the span of the parasitic period result in several generations of ammocoetes coexisting in a stream, with potentially important consequences for sea lamprey population dynamics.

The population dynamics of sea lamprey can be influenced further by sex ratio, which influences the effective population size. Sex ratios of sea lampreys in the Great Lakes have changed since lampricide applications in streams were implemented as part of the control program (Smith 1971; Potter 1980). Sex ratios were biased slightly in favour of males at the beginning of the control program, but by the end of the 1970s there were 26%–31% male in Lake Superior, 31%–39% male in Lake Huron, and 21%–44% male in Lake Michigan (Purvis 1979; Jones et al. 2003). There is no evidence that lampricides were the direct cause of these changes; rather, shifts in sex ratio may reflect a population response to reductions in abundance (Jones et al. 2003). Sex ratio influences the variance in reproductive success (Nunney 1993), and a population's ability to increase from low numbers is enhanced when females predominate (Caughley 1994).

Measurements of life history traits collated from the literature (Table 1) were used to construct a generic life table for Great Lakes sea lamprey. Sea lamprey within a Great Lake were assumed to represent one discrete population given the sea lamprey's lack of homing (Bergstedt and Seelye 1995), evidence of wide juvenile movement within each of the Great Lakes (Bergstedt et al. 2003), and the species' capacity to disperse (see Christie and Goddard 2003).

### Demographic modeling

The sea lamprey life cycle was modeled as a birth-pulse population (i.e., seasonal reproduction) and with five life stages (see Fig. 1): young of the year (YOY; stage 1), ammocoetes (larvae older than 1 year; stage 2), transformers (stage 3), parasitic juveniles (stage 4), and adults (stage 5). YOY constituted a separate larval stage as a result of the great differences (several orders of magnitude) between the survival rates of fish populations during the first year of life and the survival rates observed in subsequent years (Wootton 1996; this study). Environmental stochasticity and density dependence were included in the model. Environmental stochasticity was incorporated by defining variation ranges for the vital rates and by calculating confidence intervals (CIs) for population growth rates and population responses. Density dependence was incorporated because compensatory mechanisms have been detected in the early stages of sea lamprey's life cycle (e.g., Jones et al. 2003), even though annual abundances of spawning sea lamprey are approximately 10% of levels detected from 1940 to 1960 (Christie and Goddard 2003, and references therein). The strength of density dependence was inferred from the analysis of lake-specific time series of spawner abundance.

### Deterministic approach

The life cycle of sea lamprey was represented by a stage-structured matrix model (**M**) incorporating lake-specific vital rates (Fig. 1). Lake-specific matrices, $\mathbf{M}_{\text{Lake}}$, were constructed with vital rate data plus information on age at metamorphosis, duration of parasitic stage, and sex ratio. There is only one reproductive loop in the life cycle graph because sea lampreys are semelparous (Manion and Hanson 1980). The corresponding population projection matrix uses a 1-year projection interval, and the matrix elements represent the fecundity coefficient ($F_5$), probabilities of surviving and remaining in the same stage ($P_i$), and the transition probabilities of surviving and moving to the next stage ($G_i$). Matrix elements $F$, $P$, and $G$ were estimated from a prebreeding model where YOY would be essentially 1 year of age at the time of a hypothetical census. YOY survival rate is therefore incorporated in the fecundity coefficients (see below). As a result, matrix dimensions are reduced by one order, and $P_1$ is not explicitly incorporated in the matrix (Figs. 1*a*, 1*b*). $P_3 = 0$ because the duration of stage 3 (arrested growth and metamorphosis) is 1 year or less (Purvis 1980; Youson 2003) and therefore never longer than the projection interval, and $P_5 = 0$ because adults die after spawning and duration of this stage is less than the projection interval.

If we define $\sigma_i$ as the annual survival probability of an individual in stage $i$ and $\gamma_i$ as the probability of growth from $i$ to $i + 1$ given $\sigma_i$, then $P_i$ can be modeled as $\sigma_i(1 - \gamma_i)$ and $G_i$ as $\sigma_i\gamma_i$. The probability of leaving stage $i$ (i.e., $\gamma_i$) given that it has a fixed duration ($T_i$ in years) depends on the population's long-term growth rate and was calculated following Caswell (2001) as

$$(1) \qquad \gamma_i = \frac{(\sigma_i/\lambda)^{T_i} - (\sigma_i/\lambda)^{T_i-1}}{(\sigma_i/\lambda)^{T_i} - 1}$$

where $\lambda$ is the annual long-term population growth rate estimated from lake-specific time series. We applied the regression method of Dennis et al. (1991) to the lake-specific time series of Mullett et al. (2003) to estimate stochastic population growth rates and their variances. Population parameters generated with this method were used to estimate the mean and the 95% CIs of $\lambda$ for each lake (Table 2). The regression method assumes there is no temporal autocorrelation, which was tested through residual analysis using the Durbin–Watson statistic. Population growth parameters obtained with the regression method were used to generate three matrices for each lake representing mean, lower bound, and upper bound demographic scenarios: $\mathbf{M}_{\text{Lake, Mean}}$, $\mathbf{M}_{\text{Lake, Lower}}$, and $\mathbf{M}_{\text{Lake, Upper}}$. These matrices were therefore characterized by different values of YOY survival (see below) and different values of transition probabilities ($\gamma_i$), which are a function of the respective population growth rates $\lambda_{\text{Lake,Mean}}$, $\lambda_{\text{Lake,Lower}}$, and $\lambda_{\text{Lake,Upper}}$ (eq. 1).

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**Table 1.** Literature estimates of the mean and lower and upper bounds of variability in life history traits of Great Lakes sea lamprey (*Petromyzon marinus*).

| Trait | Estimate (lower–upper) | Source |
|---|---|---|
| Fertility (Lake Huron) | 61 500 (21 000 – 107 138) | Applegate 1950 |
| Fertility (Lake Michigan) | 62 870 (38 678 – 85 712) | Vladykov 1951 |
| Fertility (Lake Huron) | 55 913 (28 891 – 74 023) | Vladykov 1951 |
| Fertility | 55 913 (28 891 – 74 023) | Manion and McLain 1971 |
| Fertility (Lake Superior) | 68 559 (43 997 – 101 932) | Manion 1972 |
| Fertility | 34 000 – 110 300 | Scott and Crossman 1973 |
| Fertility | 68 559 (43 997 – 101 932) | Hanson and Manion 1978 |
| Fertility | 68 559(43 997 – 101 932) | Morman 1979 |
| Embryo mortality | 15% | Manion 1968 |
| Larval survival (18–21 days) | 1.10% | Scott and Crossman 1973 |
| Larval instantaneous mortality rate (all year classes) | –0.817 | Beamish et al. 1998 |
| Female egg retention | 5% | Applegate 1950 |
| Eggs successfully deposited | 14% of 95% | Applegate 1950 |
| Annual larvae survival (2–6 years) | 30%–70% | Fodale et al. 2003 |
| Duration of parasitic phase | 12–20 months | Applegate 1950 |
| Parasitic phase survival | 30%–60% | Swink 1995 |
| Parasitic phase survival | 75% | Bergstedt et al. 2003 |
| Parasitic phase survival | 65% | Young et al. 2003 |
| Reproductive pattern | Monogamy | Manion and Hanson 1980 |
| Reproductive pattern | Semelparity | Manion and Hanson 1980 |
| Downstream migration | 92% between March and June | Manion and Smith 1978 |
| Downstream migration | Fall and spring | Potter 1980 |
| Duration of ammocoete phase | 5–18 years | Manion and Smith 1978 |
| Earliest metamorphosis | Age 2 | Morkert et al. 1998 |
| Earliest metamorphosis at St. Marys River | Age 9 | Eshenroder et al. 1987 |
| Age at metamorphosis before lampricide use | Age 3 to age 5 | Beamish et al. 1998 |
| Average age at metamorphosis of established populations | 6–8 years | Potter 1980 |
| Sex ratio (prior to larvicide use) | 45% females | Potter 1980 |
| Sex ratio (Lake Ontario; prior to larvicide use) | 43% females | Potter et al. 1974 |
| Sex ratio (after treatment 1967–1972) | 74%–87% females | Potter 1980 |
| Sex ratio (Lake Superior; after treatment) | 69%–74% females | Purvis 1979 |
| Sex ratio (Lake Huron; after treatment) | 61%–69% females | Purvis 1979 |
| Sex ratio (Lake Michigan; after treatment) | 56%–79% females | Purvis 1979 |
| Duration of rest period and metamorphosis | 1 year | Purvis 1980 |
| Duration of rest period and metamorphosis | May be more than 1 year | Manion and Smith 1978 |
| Duration of rest period and metamorphosis | 4–10 months | Potter 1980 |
| Duration of metamorphosis | 10–11 months | Youson 2003 |
| Metamorphosis success (in laboratory) | 50% | Holmes and Youson 1994 |

### Estimating survival rates

Three values of YOY survival were therefore estimated for each lake using the three deterministic matrices to solve for $\sigma_1$ after computing the values of $\sigma_{2-4}$, $\gamma_{2-4}$, and fecundity ($m$) at the population growth rates estimated from the time series. This approach was selected over literature-based estimates because the limited availability and uncertainty of literature values (Table 1) for retention of eggs by spawning females, spawning success, embryo mortalities, and ammocoete survival estimates present challenges to estimating YOY survival.

Ammocoete survival probability ($\sigma_2$) was estimated by fitting the length-at-age data from Wigley (1959) to the von Bertalanffy growth model and entering the growth coefficient ($k$) into Jensen's natural mortality model (Jensen 1996): $M_2 = 1.5k$.

This generated a stage 2 survival probability of $\sigma_2 = 0.53$, which is similar to the estimate of ammocoete survival (0.56) presented by Beamish et al. (1998) and within the 30%–70% interval estimated by Fodale et al. (2003). Ammocoete transition probability ($\gamma_2$) for the deterministic matrices was calculated for a mean age at metamorphosis of 4 years (i.e., $T_2 = 3$).

Mean survival probability during metamorphosis ($\sigma_3$) was assumed to be identical to ammocoete survival (i.e., $\sigma_3 = 0.53$). This mean value for transformer survival was also similar to the 50% rate of metamorphosis success estimated by Holmes and Youson (1994). As in the case for $\gamma_1$, transformer transition probability was $\gamma_3 = 1$ because the stage duration was assumed to be exactly 1 year.

Survival probability of the parasitic phase ($\sigma_4$) was determined from Swink (1995), Young et al. (2003), and Bergstedt et al. (2003), who estimated a stage 4 survival of 30%–60%, 65%, and 75%, respectively. We assumed a mean survival rate of 60% ($\sigma_4 = 0.6$) for parasitic phase because, in general, probability of survival for juveniles is expected to

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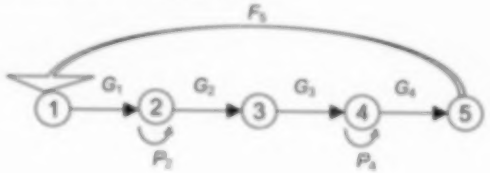
**Fig. 1.** Generalized sea lamprey (*Petromyzon marinus*) life cycle (*a*), corresponding stage-structured projection matrix (*b*), and corresponding matrix including formulas for the matrix elements in *b* (*c*). The life cycle was divided into five stages: 1, young of the year; 2, ammocoete; 3, transformer; 4, juvenile; and 5, adult. $F_i$ represents stage-specific fecundity rate, $P_i$ is the probability of surviving and remaining in the same stage, and $G_i$ is the probability of surviving and moving to the next stage. Annual survival probability of an individual in stage $i$ is $\sigma_i$, and the probability of growth from $i$ to $i + 1$ given $\sigma_i$ is $\gamma_i$.

(a)




(b)

$$\mathbf{M} = \begin{pmatrix} P_2 & 0 & 0 & F_5 \\ G_2 & 0 & 0 & 0 \\ 0 & G_3 & P_4 & 0 \\ 0 & 0 & G_4 & 0 \end{pmatrix}$$

(c)

$$\mathbf{M} = \begin{pmatrix} \sigma_2(1-\gamma_2) & 0 & 0 & m\sigma_1 \\ \sigma_2\gamma_2 & 0 & 0 & 0 \\ 0 & \sigma_3\gamma_3 & \sigma_4(1-\gamma_4) & 0 \\ 0 & 0 & \sigma_4\gamma_4 & 0 \end{pmatrix}$$

be higher than probability of survival for larvae (Wootton 1996).

Assumptions associated with using mean values for survival and transition probabilities were later relaxed by incorporating uncertainty using a stochastic model.

### Estimating fecundity rates

The fecundity coefficient ($F$) was calculated as the product of YOY survival and the number of female offspring per female per year ($m$). To facilitate how changes in sex ratio might affect fecundity estimates, the term $m$ was partitioned into fertility ($f$ = number of eggs) and proportion of adult females ($\eta$) as follows:

$$(2) \qquad F = \sigma_1 f \eta$$

We addressed the variation in sex ratios by estimating fecundity rates using a balanced sex ratio for the lower Great Lakes, Erie and Ontario (there is no evidence of female predominance in these lakes; e.g., Larson et al. 2003; Sullivan et al. 2003), and a female bias of 71% in Lake Superior, 65% in Lake Huron, and 68% in Lake Michigan.

**Table 2.** Mean and 95% confidence limits for population growth rate estimated for sea lamprey (*Petromyzon marinus*) in each Laurentian Great Lake.

| | λ | | | |
|---|---|---|---|---|
| Lake | Lower bound | Mean | Upper bound | DW |
| Superior | 0.65 | 0.94 | 1.35 | NS |
| Huron | 0.88 | 1.07 | 1.29 | NS |
| Michigan | 0.88 | 1.04 | 1.25 | NS |
| Ontario | 0.73 | 0.94 | 1.21 | NS |
| Erie | 0.64 | 0.96 | 1.43 | NS |
| All lakes | 0.94 | 1.00 | 1.07 | NS |

**Note:** The bottom row provides the population parameters obtain when lake-specific abundances are summed into a single time series (see Mullett et al. 2003). The Durbin–Watson statistic (DW) tests for temporal autocorrelation in the time series: NS represents not significant at $p = 0.05$.

### Elasticity analysis

Demographic matrices have corresponding right ($w$) and left ($v$) eigenvectors. $w$ represents the stable stage distribution, specifying the proportion of the population in stage class $i$ once enough time has passed that fluctuations due to initial conditions have finished (McDonald and Caswell 1993). $v$ represents the reproductive value of an individual in stage class $i$ (Burgman et al. 1993). Both eigenvectors are used as mathematic operators to calculate the sensitivity and elasticity of λ. The sensitivity matrix $\mathbf{Sen} = \partial\lambda/\partial a_{ij}$ provides a measure of the response of λ to perturbations in matrix elements $a_{ij}$ (Caswell 2001). It measures the impact on λ due to an infinitesimal change in matrix **A**, where the subscripts $i$ and $j$ represent the $i$th row and $j$th column of each of the matrix elements, relative to the effects of equal absolute changes in other elements. The sensitivity matrix is calculated as $(v_i w_j)/\langle w, v\rangle$, where $\langle w, v\rangle$ is the scalar product of the eigenvectors. Elasticity ($\mathbf{e}_{ij}$) measures sensitivity on a proportional scale. It is valuable because the elements $a_{ij}$ can be measured on different scales, and λ can be orders of magnitude less sensitive to changes in fecundity than to changes in survival (De Kroon et al.1986). Elasticity is calculated as

$$(3) \qquad \mathbf{e}_{ij} = (a_{ij}/\lambda)(\partial\lambda/\partial a_{ij})$$

Elasticities also quantify the contribution of $a_{ij}$ to λ and sum to unity. Thus, multiplying the set of elasticities by λ produces a set of contributions that sums to λ, and $\mathbf{e}_{ij}$ gives the relative contribution of the different transitions to λ (De Kroon et al. 1986). Equation 3 estimates the elasticities of matrix elements, not vital rates, and the latter can contribute to more than one matrix element. Elasticities of vital rates were calculated using the chain rule for differentiation:

$$(4) \qquad x/\lambda\,\partial\lambda/\partial\tau = \tau/\lambda \sum \partial\lambda/\partial a_{ij}\,\partial a_{ij}/\partial\tau$$

where τ is a lower-level variable (e.g., vital rate). Lower-level elasticities do not normally sum to one, but they still indicate the relative sensitivity of λ to changes in the life history traits and vital rates. In stage-structured matrices, the elasticity of λ to stage-specific survival ($\mathbf{e}\sigma_i$) is also calculated as the sum of elasticities to $P_i$ and $G_i$ (Doak et al. 1994; Caswell 2001).

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### Incorporating uncertainty into the vital rates

For each lake, we generated 1000 random matrices where values of vital rates were drawn from uniform distributions defined by the limits for each vital rate, as determined below (also Table 3). Values for $\lambda$, $\epsilon$, and $m$ were calculated for each matrix, and a parametric bootstrap was used to estimate 95% CIs for each $\epsilon$. All computations of $\lambda$, $\epsilon$, parametric bootstrap, and simulations were conducted using MATLAB version 7 (The Mathworks, Inc., Natick, Massachusetts).

The three values of YOY survival ($\sigma_1$) computed for each of the three lake-specific deterministic matrices were used as low, mean, and high values to define this variable's distribution in the parametric bootstrap. Corresponding transition rates ($\gamma_1$) do not vary when the stage duration equals the projection interval (i.e., 1 year). Lower and upper limits for ammocoete survival ($\sigma_2$) and transformer survival ($\sigma_3$) were assumed to be identical, with magnitudes of 0.3 and 0.7, respectively. Limit values for juvenile survival ($\sigma_4$) were set to 0.3 and 0.75. Uncertainty in age at metamorphosis was incorporated through estimates of $\gamma_2$ from the lower (1 year) and upper (5 years) limits for ammocoete stage duration based on the observed range for age at metamorphosis (2–6 years). Therefore, for the parametric bootstrap, stage durations of 5, 3, and 1 year matched with the repsective lower, mean, and upper $\lambda$ values of the deterministic matrices were used to compute $\gamma_2$ lower bound, mean, and upper bound according to eq. 1. Given that the span of the metamorphosing stage is reasonably certain, the stage was fixed at 1 year. Therefore, the transition probability ($\gamma_3$) does not vary. Uncertainty in juvenile transition probabilities ($\gamma_4$) was incorporated through changes in stage duration of 1.00, 1.33, and 1.66 years. These values were coupled according to eq. 1 with the upper, mean, and lower $\lambda$ values of the deterministic matrices to compute $\gamma_4$ upper bound, mean, and lower bound, respectively.

$m$ was assumed to depend directly on the time spent in the lake (Sawyer 1980) because fecundity increases with increasing body size (Applegate 1950), and adult body size depends on energy reserves accumulated during the parasitic phase. A newly metamorphosed sea lamprey that migrates into a Great Lake in the fall could therefore be up to three times larger at maturation than a similar individual that overwinters in the stream substrate, where it cannot feed, and migrates into the lake in the following spring (Swink 1995), thus providing a potential advantage in fecundity. Three different values of fertility ($f$ in eq. 2) were therefore used in the calculation of $m$, depending on the duration of stage 4 (i.e., 1.00, 1.33, or 1.66 years). Corresponding 95% CIs for each value were estimated using all fertility values in Table 1, without repeated estimates, and including means, maxima, and minima. The lower 95% CI bound, the mean, and the upper 95% CI bound were assigned to stage 4 durations of 1, 1.33, and 1.66 years, corresponding to fertility values of 48 565, 63 894, and 79 222, respectively. Lastly, these three levels of fertility were multiplied by the lake-specific proportion of females ($\eta$) to generate a lower bound, mean, and upper bound for $m$ for each lake.

### Perturbation analysis

We focused our simulations on how values of $\lambda$ of sea lamprey are expected to respond to reductions in lampricide use and corresponding increases in the use of alternative control methods, but a wider variety of scenarios could be simulated. The effect of suppressing $m$ via alternative controls on $\lambda$ was adjusted for density-dependent compensatory mechanisms using an index of density dependence generated for each lake (see below). We also simulated the management trade-offs between lampricide treatments and alternative control methods by constructing isoclines depicting equal $\lambda$ when trading off prejuvenile (i.e., YOY, ammocoete, and transformer stages) survival, the target of lampricides, against fecundity, the target of alternative control methods.

The consequences of management actions affecting multiple vital rates such as lampricides on $\sigma_1$, $\sigma_2$, and $\sigma_3$ can be

**Table 3.** Lake-specific means and lower and upper bounds of the variability for individual vital rates.

| Lake | Vital rate* | Lower limit | Mean | Upper limit |
|---|---|---|---|---|
| Superior | $\sigma_1$ | 0.000 26 | 0.000 37 | 0.0044 |
| | $\sigma_2$ | 0.3 | 0.53 | 0.7 |
| | $\gamma_2$ | 0.025 | 0.169 | 1 |
| | $\sigma_3$ | 0.3 | 0.53 | 0.7 |
| | $\sigma_4$ | 0.3 | 0.6 | 0.75 |
| | $\gamma_4$ | 0.447 | 0.694 | 1 |
| | $m$ | 34 481 | 45 365 | 56 248 |
| Huron | $\sigma_1$ | 0.000 24 | 0.000 92 | 0.065 |
| | $\sigma_2$ | 0.3 | 0.53 | 0.7 |
| | $\gamma_2$ | 0.009 | 0.141 | 1 |
| | $\sigma_3$ | 0.3 | 0.53 | 0.7 |
| | $\sigma_4$ | 0.3 | 0.6 | 0.75 |
| | $\gamma_4$ | 0.389 | 0.676 | 1 |
| | $m$ | 31 567 | 41 531 | 51 494 |
| Michigan | $\sigma_1$ | 0.0002 | 0.000 74 | 0.062 |
| | $\sigma_2$ | 0.3 | 0.53 | 0.7 |
| | $\gamma_2$ | 0.009 | 0.147 | 1 |
| | $\sigma_3$ | 0.3 | 0.53 | 0.7 |
| | $\sigma_4$ | 0.3 | 0.6 | 0.75 |
| | $\gamma_4$ | 0.389 | 0.68 | 1 |
| | $m$ | 33 024 | 43 448 | 53 871 |
| Ontario | $\sigma_1$ | 0.000 24 | 0.000 53 | 0.0165 |
| | $\sigma_2$ | 0.3 | 0.53 | 0.7 |
| | $\gamma_2$ | 0.017 | 0.169 | 1 |
| | $\sigma_3$ | 0.3 | 0.53 | 0.7 |
| | $\sigma_4$ | 0.3 | 0.6 | 0.75 |
| | $\gamma_4$ | 0.424 | 0.694 | 1 |
| | $m$ | 24 282 | 31 947 | 39 611 |
| Erie | $\sigma_1$ | 0.000 47 | 0.0006 | 0.0053 |
| | $\sigma_2$ | 0.3 | 0.53 | 0.7 |
| | $\gamma_2$ | 0.026 | 0.164 | 1 |
| | $\sigma_3$ | 0.3 | 0.53 | 0.7 |
| | $\sigma_4$ | 0.3 | 0.6 | 0.75 |
| | $\gamma_4$ | 0.45 | 0.69 | 1 |
| | $m$ | 24 282 | 31 947 | 39 611 |

*$\sigma_1$, YOY survival; $\sigma_2$, ammocoete survival; $\gamma_2$, ammocoete transition probability; $\sigma_3$, transformer survival; $\sigma_4$, juvenile survival; $\gamma_4$, juvenile transition probability; $m$, fecundity. Vital rates $\gamma_1$ and $\gamma_3$ are not included because they have a fixed duration of 1 year and therefore do not vary.

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**Table 4.** The number of tributaries used by sea lamprey (*Petromyzon marinus*) in each lake, the number of tributaries treated regularly (3- to 5-year cycle), the total mortality recorded in treated tributaries (including natural mortality), and the lake-wide transformer mortality attributed to lampricide treatments ($\Psi_{Lake,transformer}$).

| Lake | Sea lamprey tributaries | Tributaries treated regularly | Total mortality | Lampricide mortality ($\psi$) |
|---|---|---|---|---|
| Superior | 136 | 58 | 0.97 | 0.74 |
| Huron | 117 | 40 | 0.97 | 0.71 |
| Michigan | 121 | 35 | 0.94 | 0.43 |
| Ontario | 57 | 31 | 0.96 | 0.61 |
| Erie | 21 | 5 | 0.67 | 0.54 |

assessed promptly by adding values of $\epsilon$ (Mills et al. 1999). These consequences for $\lambda$ were calculated as

$$(5) \qquad \lambda' = \lambda(1 + \sum \epsilon_{\tau_i} \delta_{\tau_i})$$

where $\epsilon_{\tau_i}$ is the elasticity of involved vital rates $\tau_i$, and $\delta_{\tau_i}$ is the magnitude of the perturbation expressed as a proportional change.

Equation 5 approximates $\lambda$ as a linear function of $\epsilon$ and provides robust projections when perturbing the vital rates by up to 30% and occasionally to 50% (Caswell 2001). For larger perturbations, these analytical solutions become inaccurate when the relationship between a vital rate and $\lambda$ is nonlinear (see Mills et al. 1999; De Kroon et al. 2000). Results from elasticity analyses were therefore used as a first approximation to guide more accurate estimates involving direct perturbation of the projection matrices. We used direct perturbations to estimate (*i*) the success required from alternative control methods to maintain current control effectiveness when lampricide use is decreased by up to 20% and (*ii*) the level of control recommended for the worst-case scenario portrayed by the maximum values of $\lambda$ estimated in the analysis of time series for each lake.

We assumed that any reduction in lampricide use produced a similar reduction in mortality via lampricides. This assumption was considered reasonable because the high prejuvenile mortalities (95%–99%) obtained per lampricide treatment (W. Swink, US Geological Survey, Hammond Bay Biological Station, 11188 Ray Road, Millersburg, MI 49759, USA, unpublished data) and the optimized selection of streams for treatment (Christie et al. 2003) leave little room for increasing lampricide efficiency. Estimates of transformer mortality attributable to lampricides ($\Psi_{Lake,transformer}$) were made for each lake because of differences in control effort among lakes and because lampricide treatments are applied to tributaries selected for treatment based on projected juvenile production (Christie et al. 2003). To accomplish this, we used the lake-specific relationships between the larval population assessed in 2000 ($N_L$) and estimated transformed population for year 2001 ($N_T$) in tributaries treated with lampricides (Klar and Schleen 2001). Values obtained from these relationships were adjusted for natural mortality during the larval and transformer stages, assuming a mean age of metamorphosis of 4 years. $\Psi_{Lake,transformer}$ was then estimated as

$$(6) \qquad \Psi_{Lake,transformer} = 1 - [N_T(1 - \Phi)/(N_L \sigma_2^3 \sigma_3)]$$

given that the projection interval is 1 year and highly productive tributaries are treated on a regular 3- to 5-year cycle (Klar and Schleen 2001) and including the proportion of tributaries treated annually ($\Phi$) in each lake, as reported in (Klar and Schleen 2001), over a mean treatment cycle of 4 years.

Equation 6 provided $\Psi_{Lake,transformer}$ values ranging from 0.43 (Lake Michigan) to 0.74 (Lake Superior). This simple way of estimating current lampricide effects is still preferable to using a single value for all of the Great Lakes. It also has the advantage of separating natural mortality from mortality ascribed to lampricides (see Table 4), without assuming that observed mortality rates are entirely due to lampricides. Two scenarios were investigated. In general, control agents perceive that lampricide treatments affect YOY, ammocoete, and transformer survival with equal effectiveness (Christie et al. 2003). However, because streams are selected for treatment based on transformer populations, transformers might be targeted more heavily than ammocoetes and YOY, and lower mortalities might be expected for these two stages, thus reducing the lake-wide prejuvenile mortality. Recent estimates of lampricide mortalities in Lake Michigan indicated mortalities of 46% in transformers and 20% in larvae (M. Jones, Department of Fisheries and Wildlife, Michigan State University, East Lansing, MI 48824, USA, personal communication). Therefore, perturbation analyses were conducted separately for (*i*) equal lampricide mortality over all prejuvenile stages and (*ii*) lampricide mortality in larvae (YOY and ammocoetes stages) being half of that in transformers.

Increased reliance on lampricides is not proposed in the GLFC's current management plan, but was assessed here because of growing concern regarding the potential for instream barriers to fragment populations of nontarget stream fishes and growing interest in dam removal (Graf et al. 2002; Sarakinos and Johnson 2003; Cumming 2004). Our assessment determined the magnitude of control needed to keep the upper 95% confidence limit of population growth rate ($\lambda_{Upper}$) at the equilibrium value of 1. We used the upper bound instead of the mean to be conservative and embrace the worst-case scenario: mean estimates of $\lambda$ from time series analyses suggested populations were declining or growing slightly, but upper bounds were greater than 1 for all Great Lakes, suggesting that the possibility of high positive values of $\lambda$ remains. Analysis for this assessment was done using eq. 7 and later refined using direct perturbations of projection matrices.

$$(7) \qquad \delta_{\tau_i} = (1/\epsilon_{\tau_i})[(1 - \lambda_{Upper})/\lambda_{Upper}]$$

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### Incorporating density dependence

Density dependence in fish populations generally focuses on compensatory mechanisms in YOY survival (Ricker 1975; DeAngelis et al. 1980; Levin and Goodyear 1980). We therefore incorporated density-dependent effects on YOY survival, ignoring other potential compensatory mechanisms such as shifts in host–parasite ratios with declining sea lamprey abundance, because these other mechanisms were not considered relevant to comparisons between lampricide treatment and alternative controls (e.g., Jones et al. 2003). YOY survival ultimately depends on the number of spawners and was considered overcompensatory, given that the number of suitable nesting sites could be limited. High egg densities can deplete oxygen and decrease egg survival, as well as potentially increase hatchling competition for food and space (Morris and Doak 2002). We used the Ricker function in the fecundity coefficient of the matrix model ($F_1 = \xi_d m$) to model proportional increases in YOY survival arising through proportional reductions in fecundity ($\delta_m$) as

$$\xi_d = \sigma_1(1 + \delta_m e^{-\beta \delta_m}) \quad (8)$$

where $\xi_d$ is the density-dependent YOY survival, and $\beta$ is the index of density dependence. Time series of spawner abundances comprising the years 1977–1999 (Mullett et al. 2003) were used to determine the strength of density dependence from the relationship between spawner abundance and population growth rate expressed as $\log_e(N_{t+x}/N_t)$ (Turchin 1995), where $x$ is the time lag associated with $\lambda$ as a function of age at reproduction (Holmes 2001). Lags of 4, 5, 6, 7, and 8 years were considered, given that durations of metamorphosis and parasitic stages are approximately 1 year each and age at metamorphosis ranges from 2 to 6 years in the Great Lakes. For each lag, we estimated the corresponding linear regression coefficients ($\beta$) and tested the statistical significance of $\beta$ being different from 0. $\beta$ values significantly different from zero at $p < 0.05$ were used to generate a unique mean $\beta$ value per lake (see Table 5). This approach, which is analogous to using a partial rate correlation function as a probe for density-dependent time lags (see Turchin 2003), was particularly appropriate given the small variation of $\beta$ values within each lake. We used $m$ instead of the number of the spawners in this analysis because at the population level, any reduction in the proportion of spawners eliminated from a semelparous population represents an identical proportional reduction in fecundity rates (see L.A. Vélez-Espino, R.L. McLaughlin, M.L. Jones, and T.C. Pratt, unpublished data). Ranges of the density-dependent effects on $\lambda$ arising via changes in $m$ were summarized by predictive equations (Table 6) that facilitated simulation of specific management scenarios involving perturbations of fecundity rates.

Henceforth we refer to baseline fecundity as the annual number of spawner females successfully reproducing in an individual lake under current suppression of fecundity via alternative control methods. Similarly, we refer to baseline prejuvenile survival as the lake-specific annual survival rate of prejuvenile lampreys after consideration of natural mortality and mortality via lampricide treatments. Finally, we refer to baseline lampricide use as the annual number of lampricide treatments and amount of lampricide accounting for the lake-specific, prejuvenile mortality (Table 4). Under the assumption that lampricide efficiency has been maximized by the control program, any increase in baseline lampricide use (maintaining current efficiency) is therefore expected to produce a proportional reduction in baseline prejuvenile survival. The effect on $\lambda$ of proportional increases in baseline lampricide use ($z$) was computed through direct perturbation of the matrix $\mathbf{Z}$:

$$\mathbf{Z} = \begin{pmatrix} \sigma_2(1-z)(1-\gamma_2) & 0 & 0 & m\sigma_1(1-z) \\ \sigma_2\gamma_2(1-z) & 0 & 0 & 0 \\ 0 & \sigma_3\gamma_3(1-z) & \sigma_4(1-\gamma_4) & 0 \\ 0 & 0 & \sigma_4\gamma_4) & 0 \end{pmatrix} \quad (9)$$

## Results

### Inferences from elasticity analysis

Values of vital rate elasticities generated by the deterministic matrices were similar across Great Lakes and indicated that lake-specific sea lamprey population growth rates were more sensitive to proportional changes in ammocoete survival than to changes in survival rates of the remaining life stages or to changes in fecundity (Fig. 2). Elasticities for ammocoete survival ranged from 0.25 to 0.38, and a 10% decrease in this vital rate is expected to reduce $\lambda$ by 2.5%–3.8%. Survival of the juvenile–parasitic stage was next highest and had the lowest variation in $\epsilon$ (0.25 to 0.26). A 10% decrease in juvenile survival is expected to reduce $\lambda$ by 2.5%–2.6%. Remaining vital rates exhibited identical elasticities across lakes because of the fixed projection interval (1 year) for YOY and transformer stages, and because sea lampreys are semelparous. Elasticities of YOY survival, transformer survival, and fecundity ranged from 0.18 to 0.25, indicating that a 10% decrease in any of these vital rates is expected to produce a 1.8%–2.5% decrease in the $\lambda$.

Analysis of elasticities from the model incorporating environmental stochasticity provided qualitatively similar conclusions. Mean values of $\epsilon$ for the stochastic matrices were similar to those produced by the deterministic matrices, with the exception of ammocoete survival where stochastic elas-

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**Table 5.** Index of density dependence (β) computed for each lake from linear regression coefficients between spawner abundance and population growth rate using different time lags to account for the range of observed age at reproduction.

| Lake | Lag (years) | β | $R^2$ | $P$ | Mean β |
|---|---|---|---|---|---|
| Superior | 4 | –0.0097 | 0.42 | 0.0088 | –0.009 53 |
| | 5 | –0.0065 | 0.20 | 0.1083 | |
| | 6 | –0.0068 | 0.28 | 0.0619 | |
| | 7 | –0.0086 | 0.40 | 0.0275 | |
| | 8 | –0.0103 | 0.42 | 0.031 | |
| Huron | 4 | –0.0044 | 0.69 | <0.0001 | –0.006 06 |
| | 5 | –0.0056 | 0.81 | <0.0001 | |
| | 6 | –0.007 | 0.91 | <0.0001 | |
| | 7 | –0.0063 | 0.72 | <0.0001 | |
| | 8 | –0.007 | 0.74 | <0.0001 | |
| Michigan | 4 | –0.0144 | 0.61 | <0.0001 | –0.0126 |
| | 5 | –0.0107 | 0.49 | 0.0012 | |
| | 6 | –0.0129 | 0.54 | 0.0008 | |
| | 7 | –0.0123 | 0.56 | 0.0009 | |
| | 8 | –0.0127 | 0.41 | 0.0096 | |
| Ontario | 4 | –0.003 | 0.22 | 0.0505 | –0.005 95 |
| | 5 | –0.0058 | 0.52 | 0.0011 | |
| | 6 | –0.0076 | 0.66 | 0.0001 | |
| | 7 | –0.0061 | 0.50 | 0.0031 | |
| | 8 | –0.0043 | 0.40 | 0.015 | |
| Erie | 4 | –0.0864 | 0.39 | 0.0095 | –0.104 28 |
| | 5 | –0.0806 | 0.35 | 0.0201 | |
| | 6 | –0.1163 | 0.60 | 0.0012 | |
| | 7 | –0.1198 | 0.54 | 0.0045 | |
| | 8 | –0.1183 | 0.56 | 0.0049 | |

ticities were smaller than the deterministic elasticities (see Fig. 2). Despite this difference, elasticities from the deterministic models were encompassed within the 95% CIs for elasticities from the stochastic models. Confidence intervals were relatively small, except those for ammocoete survival, where wider CIs were the result of the variation in age at metamorphosis. Variation in the elasticity of ammocoete survival was greater in Lake Superior (0.29 to 0.40) than in other lakes and lowest in Lake Huron (0.27 to 0.33).

It is not possible to identify one vital rate as being the most influential on population growth rates given the similarity and uncertainty in the elasticity estimates. Nevertheless, the effect of lampricide treatments on population growth rates is expected to be approximately three times greater than the effect of alternatives controls, because lampricides affect three vital rates, survival probabilities of YOY, ammocoetes, and transformers, whereas alternative methods affect one vital rate, fecundity. This relationship is expected to hold for perturbations of up to 30% because elasticity analysis assumes a linear relationship between λ and the vital rates before and after perturbation (eq. 5) (Caswell 2001).

### Inferences from direct perturbation under density dependence

Relationships quantifying the trade-offs between mortality achieved via lampricide and via the suppression of reproduction were generated by directly perturbing the projection matrices incorporating density-dependent effects. These trajectories reflect the reduction in baseline fecundity needed to compensate for increased prejuvenile survival arising from reductions in lampricide use (Fig. 3*a*). Trajectories for each Great Lake indicated that large reductions in reproductive success will be initially needed to compensate for small reductions in mortality via lampricide treatments. The required level of fecundity suppression increases, at a decreasing rate, as the mortality achieved via lampricide use decreases. The changes become more obvious when expressed relative to current levels of larval mortality via lampricides and baseline fecundity (Figs. 3*b*, 4). Trajectories for different Great Lakes were parallel but, for a given reduction in mortality achieved via lampricides, a greater compensatory suppression of fecundity is predicted to be required for Lakes Superior and Huron than for Lake Michigan. For the first scenario with even lampricide mortality over YOY, ammocoetes, and transformers, a 20% lake-wide reduction in baseline lampricide use will require reducing baseline fecundities by 59%–67% in Lake Superior, 58%–64% in Lake Huron, 49%–53% in Lake Michigan, 55%–61% in Lake Ontario, and 54%–60% in Lake Erie to maintain the effectiveness of sea lamprey control at current levels (Fig. 3*b*). When lampricide mortality in YOY and ammocoetes is considered to be half of that in transformers, a 20% lake-wide reduction in baseline lampricide use will require 83%–85% of the levels computed for the first scenario (Fig. 4).

**Table 6.** Lake-specific polynomial equations predicting the proportional reduction in population growth rate ($y$) as a function of the proportional reduction in baseline fecundity ($x$) with density-dependent compensation in young-of-the-year (YOY) survival.

| Lake | Predictive equation | $R^2$ |
|---|---|---|
| Superior | $y = -0.5484x^3 + 0.2799x^2 - 0.1295x + 1.0064$ | 0.97 |
| Huron | $y = -0.5319x^3 + 0.2247x^2 - 0.0992x + 1.003$ | 0.98 |
| Michigan | $y = -0.5383x^3 + 0.2341x^2 - 0.1015x + 1.0031$ | 0.98 |
| Ontario | $y = -0.5208x^3 + 0.2232x^2 - 0.0983x + 1.0029$ | 0.97 |
| Erie | $y = -0.5308x^3 + 0.2432x^2 - 0.0979x + 1.003$ | 0.97 |

### Sea lamprey control under worst-case scenarios

Mean λ estimated from time series of spawner abundances suggest sea lamprey populations are declining or growing slowly, but based on the uncertainty in the estimates, annual increases of 21%–43% could occur infrequently in individual lakes (Table 2). Projected relationships between mean population growth rate and the suppression in baseline fecundity were curvilinear (Fig. 5*a*). Similar curvilinear patterns were observed for lower and upper estimates of λ. These convex trajectories indicate that the reduction in λ increases, at an increasing rate, as suppression in $m$ increases. Only when suppression of $m$ is high, >70% of baseline levels, do population responses diverge among lakes, with Lakes Michigan and Huron responding more strongly than Lakes Superior, Ontario, and Erie. Baseline $m$ would have to be reduced by 83% in Lake Superior, 79% in Lake Huron, 76% in Lake Michigan, 72% in Lake Ontario, and 88% in Lake Erie to ensure long-term λ are declining or stable given the current levels of uncertainty (Fig. 5*b*) and other things

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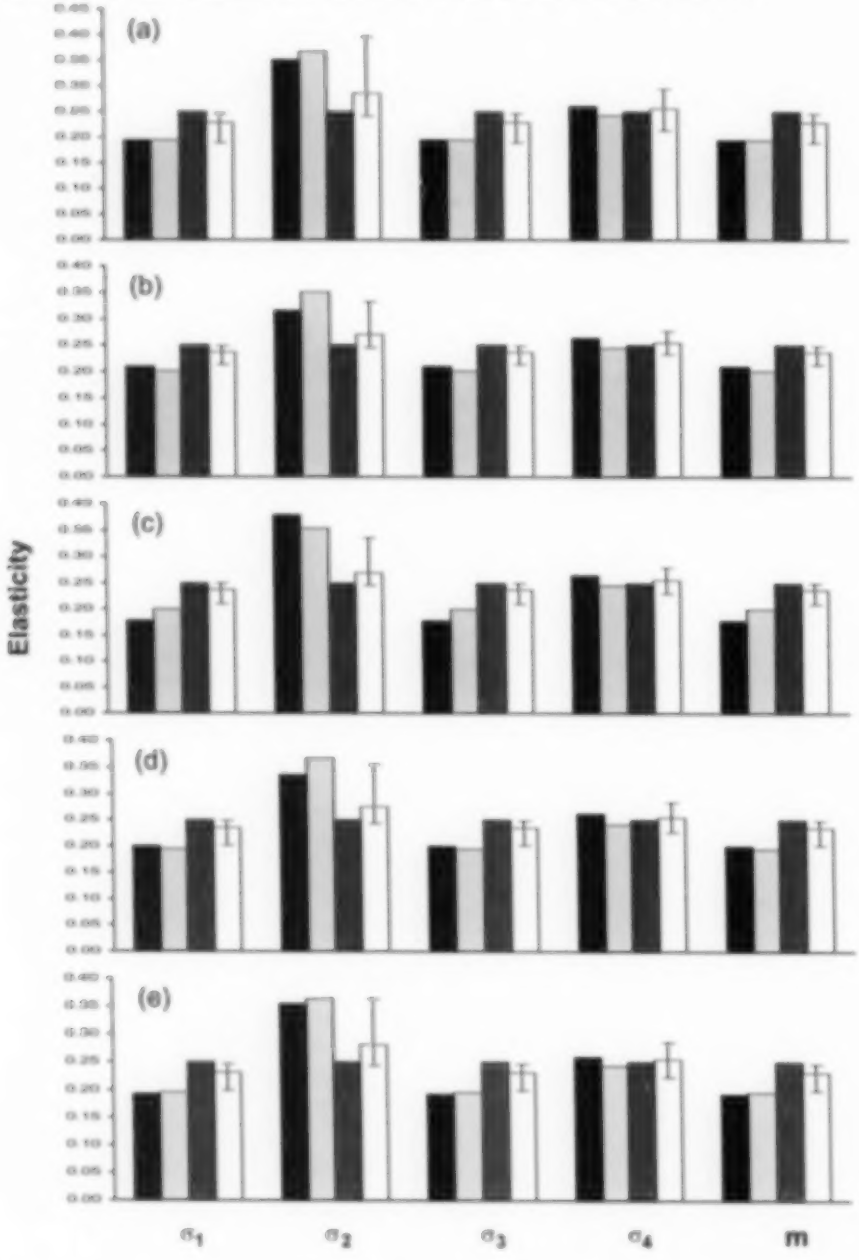
**Fig. 2.** Elasticities of vital rates calculated from deterministic and stochastic models of sea lamprey (*Petromyzon marinus*) population dynamics in each Great Lake. (*a*) Lake Superior; (*b*) Lake Huron; (*c*) Lake Michigan; (*d*) Lake Ontario; (*e*) Lake Erie. $\sigma_1$, young-of-the-year (YOY) survival; $\sigma_2$, ammocoete survival; $\sigma_3$, transformer survival; $\sigma_4$, juvenile (parasitic phase) survival; *m*, fecundity. Black bars show deterministic elasticities computed with the projection matrix $\mathbf{M}_{\text{Lake, Lower}}$. Light grey bars indicate deterministic elasticities computed with the projection matrix $\mathbf{M}_{\text{Lake, Mean}}$. Dark grey bars show deterministic elasticities computed with the projection matrix $\mathbf{M}_{\text{Lake, Upper}}$. Open bars show stochastic elasticities. 95% confidence intervals are show for open bars only.




being equal (e.g., mortality achieved via lampricides is maintained at current levels).

Projected relationships between mean λ and the baseline prejuvenile survival were linear and similar across lakes (Fig. 6*a*). Differences in population responses for individual lakes were projected to increase with increased reductions in prejuvenile survival. At high levels of prejuvenile mortality, the absolute reduction of λ in Lake Erie is expected to be

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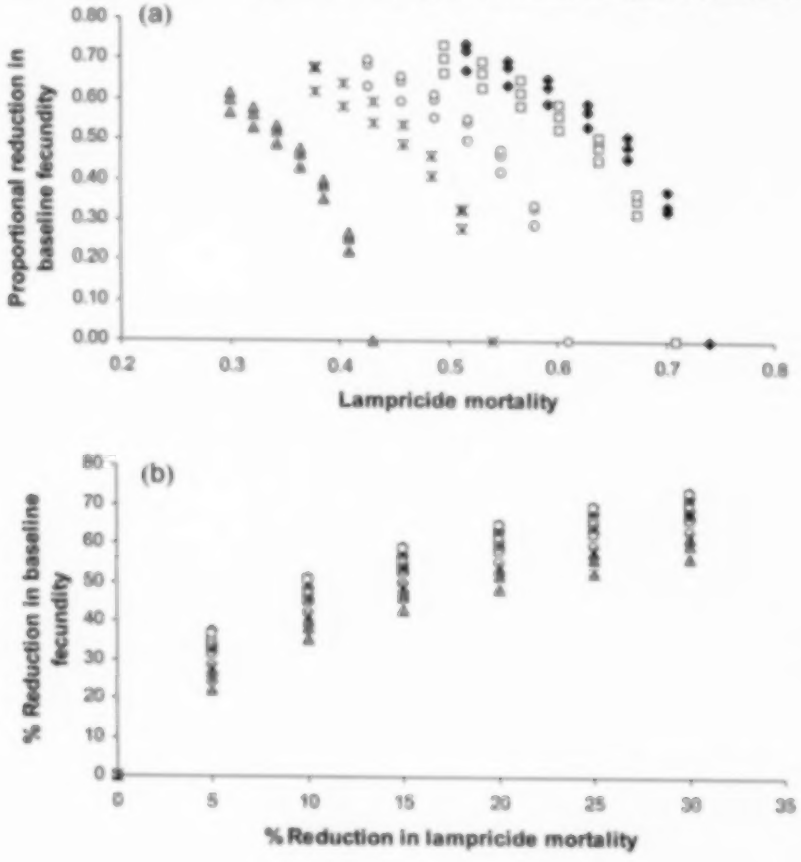
**Fig. 3.** Changes in baseline fecundity in relation to the level of prejuvenile mortality achieved via lampricide treatments when they affect evenly young-of-the-year (YOY), ammocoete, and transformer stages. (*a*) Proportional reduction in baseline fecundity needed to maintain current levels of sea lamprey (*Petromyzon marinus*) control after reducing lampricide mortality. (*b*) Relative reduction in baseline fecundity needed to maintain current levels of sea lamprey control in relation to relative reduction in lampricide mortality. The three levels depicted for each lake represent the projections generated with projection matrices $\mathbf{M}_{\text{Lake, Mean}}$, $\mathbf{M}_{\text{Lake, Lower}}$, and $\mathbf{M}_{\text{Lake, Upper}}$. Diamonds, Lake Superior; squares, Lake Huron; triangles, Lake Michigan; circles, Lake Ontario; stars, Lake Erie.




greater than the reductions expected for other Great Lakes. Baseline prejuvenile survival would have to be reduced by 32% in Lake Superior, 28% in Lake Huron, 25% in Lake Michigan, 22% in Lake Ontario, and 38% in Lake Erie to ensure that populations are declining or stable given the current levels of uncertainty (Fig. 5*b*) and other things being equal (e.g., suppression in fecundity achieved via alternative methods is maintained at current levels).

In terms of mortality achieved via lampricides, for the scenario with even lampricide mortality over YOY, ammocoetes, and transformers, baseline lampricide use would have to be increased by 44% in Lake Superior, 41% in Lake Huron, 60% in Lake Michigan, 37% in Lake Ontario, and 70% in Lake Erie to ensure populations are declining or stable given the current levels of uncertainty (Fig. 7*a*) and other things being equal (e.g., suppression in fecundity achieved via alternative methods and the efficiency of lampricide treatments are maintained at current levels). Baseline lampricide use increased by 48%–50%, relative to the levels computed in the first scenario, when lampricide mortality in YOY and ammocoetes was assumed to be half of that in transformers (Fig. 7*b*).

## Discussion

Three important management conclusions emerge from our demographic analysis. First, from a population dynamics perspective, it appears feasible to maintain current levels of sea lamprey control while decreasing reliance on chemical lampricides targeting larval life stages of sea lamprey and increasing reliance on alternative control methods targeting adult reproduction. Second, if reductions in TFM use coincide with proportional reductions in the mortality of larval sea lamprey via lampricides, then proportionally large investment in control methods suppressing reproduction will be needed to offset proportionally small reductions in methods suppressing larval survival. Our results indicate that to reach the management target of reducing the use of lampricides by 20% while preserving current control levels, it

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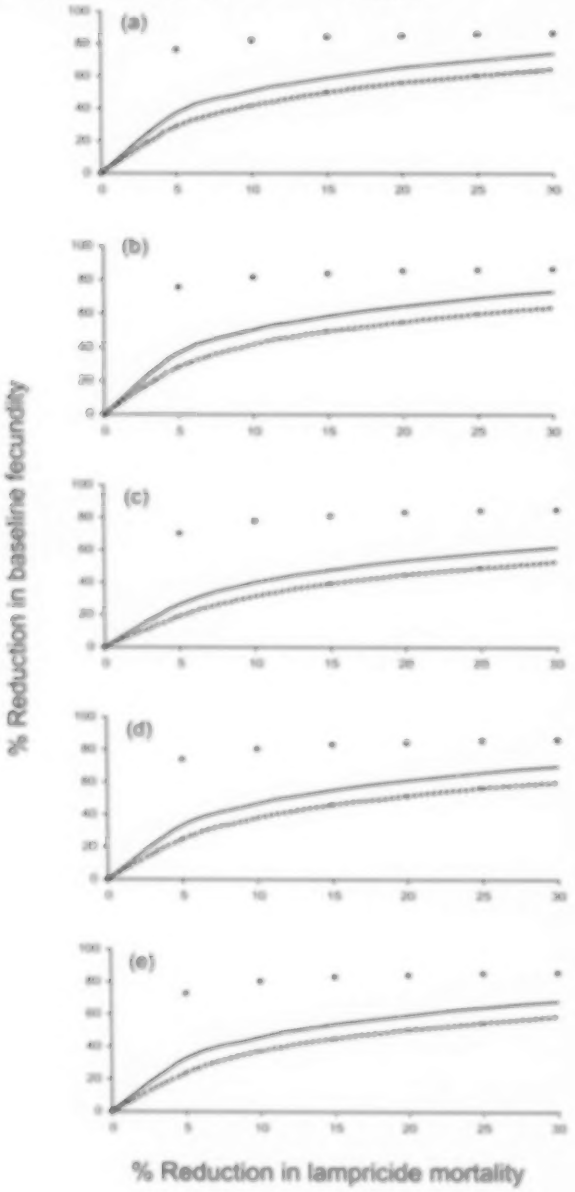
**Fig. 4.** Relative reductions in baseline fecundity needed to maintain current levels of sea lamprey (*Petromyzon marinus*) control in relation to relative reduction in lampricide mortality when lampricide mortality is the same on young-of-the-year (YOY), ammocoete, and transformer stages (continuous line) and when lampricide mortality on YOY and ammocoetes is half of that on transformers (broken line) for Lake Superior (*a*), Lake Huron (*b*), Lake Michigan (*c*), Lake Ontario (*d*), and Lake Erie (*e*). Diamonds indicate the ratio between the two scenarios. Projections were generated with projection matrix $\mathbf{M}_{\text{Lake, Mean}}$.




would be necessary to achieve an additional reduction in baseline fecundity rates ranging from 49% (Lake Michigan) to 65% (Lakes Superior and Huron) if it is the case that lampricide are equally effective to kill larvae and transformers. However, additional reduction in baseline fecundity decreases to 42%–55% when lampricide mortality on larvae is assumed to be half of that on metamorphosing individuals. Third, given current levels of uncertainty in estimated population growth rates, large suppression of prejuvenile survival or fecundity is recommended if managers want to guard against infrequent periods of high population growth. Below, we discuss how these conclusions arise from our analyses and their importance to the management of sea lamprey in the Laurentian Great Lakes.

Our analyses provided two other pertinent results. The analyses demonstrate that from a biological perspective, lampricide is unlikely to be replaced as the core method of sea lamprey control in the integrated management plan because having similar vital rate sensitivities to perturbations (i.e., elasticities), sea lamprey population growth rates are about three times more responsive to lampricides targeting simultaneously YOY, ammocoete, and transformer life stages than alternative methods targeting just reproduction. In addition, this similarity of elasticities across life stages demonstrates that expanding the suite of alternative controls to include methods targeting the parasitic, juvenile stage would be worthwhile. No current control method targets this life stage effectively (Jones et al. 2003). Traps targeting recently metamorphosed lampreys as they migrate downstream might be considered (Smith and Swink 2003).

Our first conclusion, that suppression of adult reproduction is a feasible control alternative, arises from our analyses demonstrating that elasticities are similar in magnitude across life stages, and therefore the vital rates corresponding to each life stage contribute roughly equally to population growth rate. This is not a trivial conclusion. The elasticity of fecundity could have been substantially smaller than the elasticities of other vital rates. Several North American freshwater fishes have life histories where the fecundity elasticities are substantially low relative to elasticities for juvenile survival (Vélez-Espino et al. 2006). If this were true for sea lamprey, suppression of fecundity would have much lower potential as a target for alternative control methods. Moreover, demonstrating the biological feasibility of control methods targeting reproduction is not only important for rigorously assessing the potential to exploit existing alternative controls, but also for anticipating the potential effectiveness of active, ongoing efforts to enhance the trapping of sea lamprey returning to rivers to spawn and the effectiveness of releasing sterile males (Sorensen and Vrieze 2003; Twohey et al. 2003).

Our second main conclusion, that proportionally large investment in control methods suppressing reproduction will be needed to offset proportionally small reductions in methods suppressing larval survival, is the outcome of two processes. First, lampricides target three life stages while alternative controls target only one life stage. Second, the relationship between the suppression in reproduction required to compensate for reductions in lampricide use, without compromising the overall level of control achieved, is nonlinear. Other things being equal, the nonlinear relationship suggests that if sea lamprey managers opt to increase reliance on alternative controls to reduce reliance on lampricides, they should do so vigorously, given that the recommended level of suppression in adult reproduction increases, at a decreasing rate, as the re-

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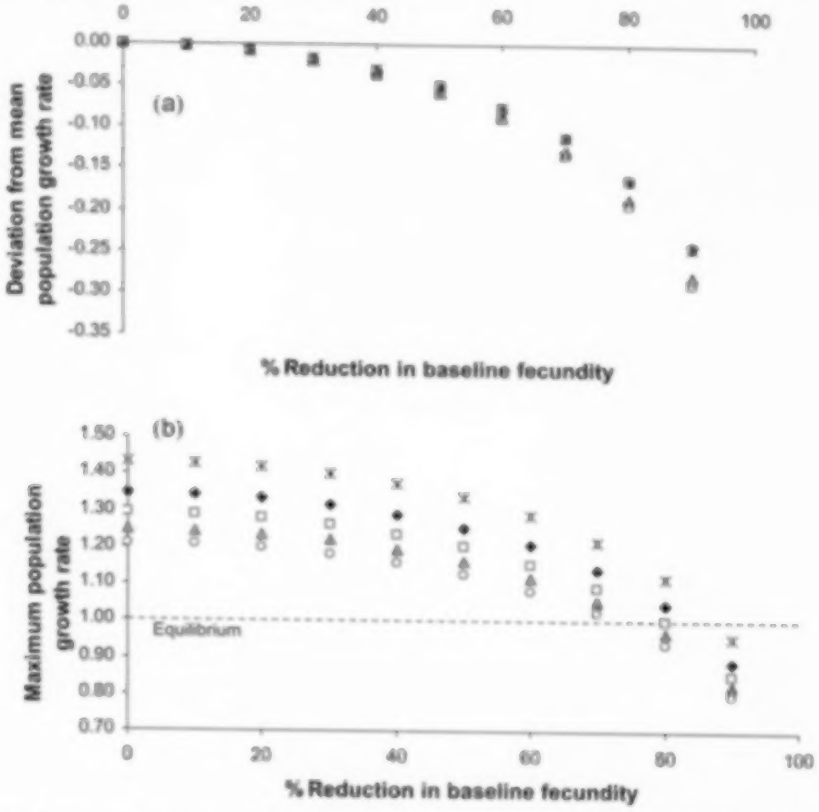
**Fig. 5.** Responses of population growth rates to increased suppression of baseline fecundity for each Great Lake. (*a*) Deviation (in λ units) from mean population growth rate ($\lambda_{Mean}$) in response to increased suppression of baseline fecundity. (*b*) Responses of maximum population growth rate ($\lambda_{Upper}$) to increased suppression of baseline fecundity. Diamonds, Lake Superior; squares, Lake Huron; triangles, Lake Michigan; circles, Lake Ontario; stars, Lake Erie.




ductions in lampricide increase. Strong year classes arising via density-independent processes may still result on occasion (Haeseker et al. 2003; Jones et al. 2003).

Interest in dam removals and the provisioning of fish passageways is heightening within the basin and across the globe (Graf et al. 2002; Sarakinos and Johnson 2003; Cumming 2004). As yet, the trade-off between using in-stream barriers to control the spread and reproduction of nonnative species and the removal of in-stream barriers to facilitate movements of native fishes is just beginning to be recognized for sea lamprey control (L.A. Vélez-Espino, R.L. McLaughlin, M.L. Jones, and T.C. Pratt, unpublished data) and more broadly (Poff and Hart 2002; Levey et al. 2005; Proches et al. 2005). In addition to its own barrier inventory, the GLFC and its contract agents monitor over 100 de facto dams that function as sea lamprey barriers, but were built for another purpose and are owned and operated by other corporations and agencies (Burkett et al. 2004). Altering these structures in ways that facilitate sea lamprey passage could hinder efforts to control sea lamprey within the Great Lakes given that alternative controls could account for as much as 25% of the overall effect achieved via an integrated management plan targeting equally all vital rates, excepting survival of the parasitic stage.

Our third conclusion that control efforts should be increased further to minimize the possibility of high annual growth rates within a lake is based on current estimates of uncertainty associated with empirical estimates of population growth rates. The sources of the uncertainty and their importance remain prominent research needs, but likely include (*i*) variation in the precision and accuracy of estimated abundances of spawners, which are obtained via a combination of mark–recapture methods on some streams and predictions made from watershed area and history of lampricide treatment on others (Mullett et al. 2003), (*ii*) variation in the effectiveness of lampricide treatments between individual applications (Christie et al. 2003) and among the three prejuvenile stages, and (*iii*) density-dependent and -independent variation in recruitment (Jones et al. 2003). To minimize the possibility of observing infrequent high population growth rates, our projections indicate it would be necessary to reduce lake-wide baseline fecundities by 72%–88% while keeping current mortality attained via lampricides. Alternatively, one could reduce baseline prejuvenile survival by 22%–38% by increasing baseline lampricide use to levels ranging from 37% (Lake Ontario) to 70% (Lake Erie) while keeping current suppression of fecundity and assuming equal lampricide mortality over all prejuvenile stages. When lampricide mortality on larvae is assumed to be half of that on transformers, baseline lampricide use would have to be increased by 55%–104% to keep sea lamprey populations at

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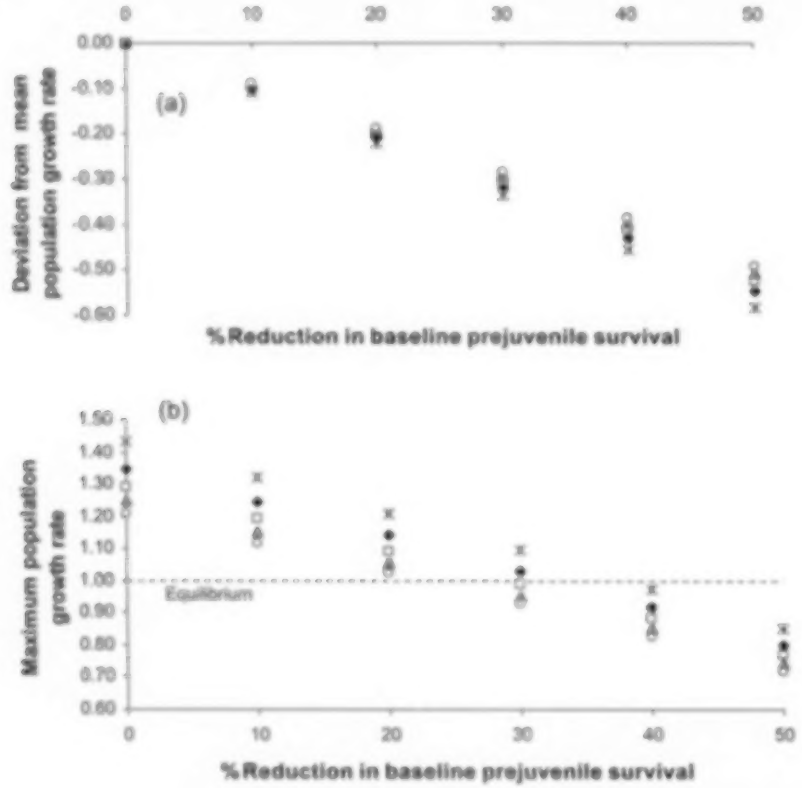
**Fig. 6.** Responses of population growth rate to changes in baseline prejuvenile survival. (*a*) Deviation (in $\lambda$ units) from population growth rate in response to increased reduction of baseline prejuvenile survival. (*b*) Responses of maximum population growth rate ($\lambda_{Upper}$) to increased reduction of baseline prejuvenile survival. Diamonds, Lake Superior; squares, Lake Huron; triangles, Lake Michigan; circles, Lake Ontario; stars, Lake Erie.




equilibrium. There are at least four reasons why these estimates should be considered prior to management decisions. First, sea lamprey populations in the Great Lakes have not yet been suppressed to target levels. Second, annual estimates of population growth rates will remain variable. Third, managers can expect to periodically observe annual estimates of positive population growth as high as 21%–43%. Fourth, the decision judged best when uncertainty is considered often differs from the decision judged when uncertainty is not considered (Clemen 1996).

Development of population dynamics models evaluating the feasibility and allocation of control strategies remains a high research priority to support sea lamprey management in the Great Lakes (Jones 2006), despite the contributions of earlier efforts to model sea lamprey population dynamics (e.g., Walters et al. 1980) and to assess the effectiveness of alternative controls versus lampricide (Haeseker et al. 2003; Jones et al. 2003). Our analyses represent an initial attempt to address this need explicitly and rigorously on a lake-wide scale. One novel feature of our approach is the application of perturbation analysis, which offers a method of directly assessing the anticipated effects of control options targeting specific life stages. Such assessments have been desired since the GLFC adopted an integrated pest management approach (Sawyer 1980; Christie and Goddard 2003). Moreover, the contrast between deterministic and stochastic models demonstrated that the population dynamics of sea lamprey can be modeled reasonably well using a deterministic matrix model. Interpretation of elasticities following incorporation of uncertainty in the vital rates led to conclusions qualitatively similar to those reached when uncertainty was not considered in the model and when approximations from elasticities were replaced by projections derived by direct perturbations of the transition matrices. Verifying these outcomes is important. Vital rates with low elasticity but high coefficients of variation can have effects on population growth rate that are as important as vital rates with high elasticities (Mills et al. 1999, 2001), though this is not always the case (De Kroon et al. 2000; Ehrlén et al. 2001). Approximations of population growth rates projected using elasticities can also differ from values obtained through direct perturbation of the transition matrices (Mills et al. 1999; De Kroon et al. 2000). In addition, our study shows that the deterministic model will perform well, without considering density-dependent survival of larvae, providing perturbations of fecundity rates are less than 40%.

As with any modeling approach, ours also has limitations and it is important to recognize these and their implications. An obvious limitation surrounds uncertainty in parameter estimates used in the models. Despite over 40 years of sea

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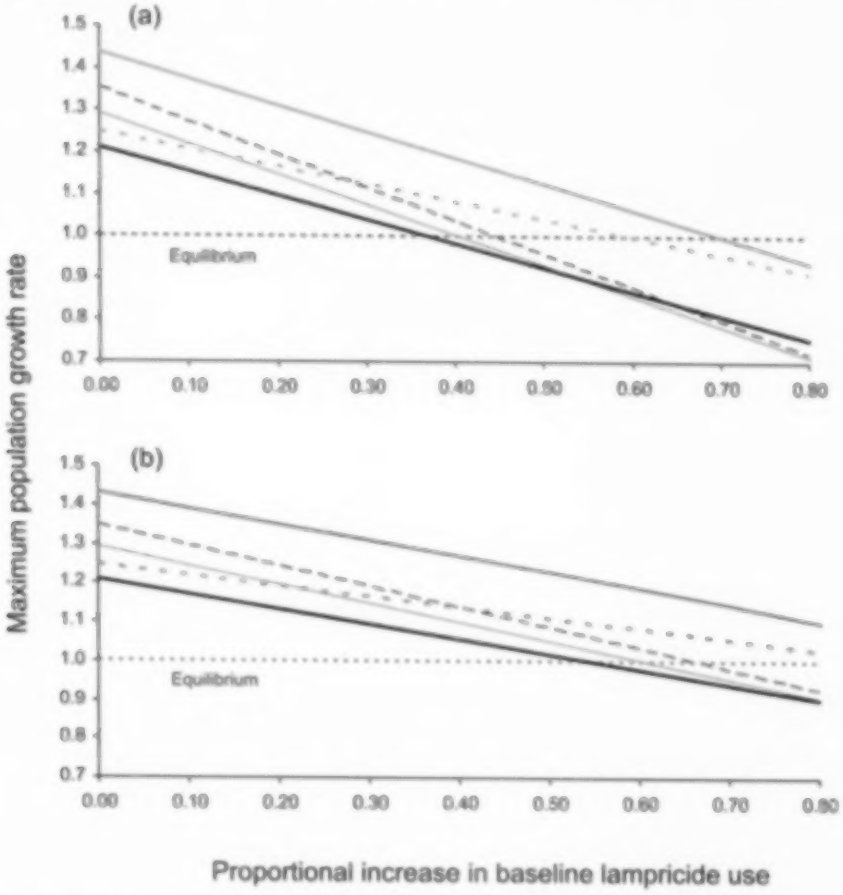
**Fig. 7.** Responses of maximum population growth rate ($\hat{\lambda}_{Upper}$) to proportional increases of baseline lampricide use: (*a*) equal lampricide mortality on young-of-the-year (YOY), ammocoete, and transformer stages; (*b*) lampricide mortality on YOY and ammocoetes being half of that on transformers. Broken black line, Lake Superior; thin grey line, Lake Huron; broken grey line, Lake Michigan; black line, Lake Ontario; thick grey line, Lake Erie.




lamprey research in the Great Lakes, knowledge of the demographics of sea lamprey during their first year of life and of variation in their age at metamorphosis remains incomplete (Jones 2006). Changes in mean and variance of parameters related to these life stages could influence projections of vital rates by altering the intensity of density dependence, the transition probabilities from ammocoete to transformer, and the CIs of elasticity for ammocoete survival in the stochastic model. There is also uncertainty associated with the levels of mortality caused by lampricides in the three modeled prejuvenile stages. Our models considered only two plausible scenarios: lampricide treatments affecting YOY, ammocoetes, and transformer survival with equal effectiveness and lampricide mortality in larvae being half of that in transformers, with empirical estimates of lake-wide transformer mortalities ranging from 43% in Lake Michigan to 74% in Lake Superior. Another limitation is the assumption that decreases in lampricide use translate into corresponding decreases in larval mortality via lampricides. Much of the early 30% reduction in TFM use (GLFC 2001) was achieved via measures taken to minimize the amount of chemical used while still achieving minimum lethal concentrations (Brege et al. 2003). However, the management agencies have now reached a stage where additional reductions in lampricide use will likely need to be compensated by suppression via other control methods. One last limitation is that our modeling effort addresses what is potentially possible from a biological perspective; it does not consider the feasibility or economics of alternative controls even though the GLFC is determining economic injury levels (EILs) for each lake (Koonce et al. 1993; Larson et al. 2003; Sullivan et al. 2003). The EIL is defined as the level of control where a marginal increase in cost of control exceeds the marginal economical benefit resulting from the added control (Sawyer 1980). Understanding of sea lamprey population dynamics is a critical ingredient for successfully implementing control based on EILs.

The sea lamprey control program in the Laurentian Great Lakes helps maintain the health of one of the largest and most valuable freshwater ecosystems in the world (Taylor and Ferrari 1999). Resources supporting the control program are limited, and managers face challenging decisions about how to

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allocate these resources between sea lamprey assessment and control and among different methods of control. These decisions are made in the presence of uncertainty about how various control decisions will alter the population dynamics of sea lamprey, particularly at the whole-lake level, and therefore determine the damage sea lamprey cause to fishes of economic and societal importance (Jones 2006). The contributions made here regarding the biological potential of different methods of sea lamprey control and the allocation between use of lampricides and alternative controls constitute a progress in the understanding of the interdynamics between sea lamprey populations and management options that will help the GLFC achieve its vision of delivering a sea lamprey management program that is environmentally and economically sound and socially acceptable. Further steps to reduce uncertainty in population parameters and increase the relevance of quantitative conclusions would be beneficial before a full implementation of our management recommendations is undertaken.

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# Landscape influences on stream fish assemblages across spatial scales in a northern Great Plains ecoregion

**Henry F. Wilson and Marguerite A. Xenopoulos**

**Abstract:** We examined the relationship between multiple spatial scales of fish assemblage structure and land cover in streams of a northern Great Plains ecoregion. We used regional richness measurements, an index of biotic integrity (IBI), and nonmetric multidimensional scaling (NMS) ordination to characterize fish assemblages. These metrics were related to regional catchment landscape at two spatial scales (overall catchment, overall riparian) and then to a set of local subcatchments from within these catchments at three scales (overall subcatchment, overall riparian buffer, and reach). Relationships between catchment fish richness, IBI scores, and landscape predictors were strongest at the riparian scale, with the strongest single predictor being riparian forest ($r^2 = 0.63$, $P < 0.01$). NMS ordination analysis showed clear similarities between fish species assemblages in agriculturally dominated catchments and assemblages found in smaller headwater streams. At the same time, forested catchments and catchments with larger areas exhibited similar fish species assemblages. Our results indicate that both local and regional stream fish assemblages are structured by broader-scale landscape characteristics, with land cover providing a better indication of overall available habitat volume than catchment area or stream order.

**Résumé :** Nous examinons la relation entre les différentes échelles spatiales de la structure des peuplements de poissons et la couverture des terres dans des cours d'eau de l'écorégion des grandes plaines boréales. Nous caractérisons les peuplements de poissons à l'aide de mesures de la richesse régionale, d'un coefficient d'intégrité biotique (IBI) et d'une ordination par cadrage multidimensionnel non métrique (NMS). Nous relions ces métriques au paysage régional du bassin versant à deux échelles spatiales (bassin versant global, zone riveraine globale) et ensuite à un ensemble de sous-bassins locaux au sein de ces bassins à trois échelles (sous-bassin versant global, zone tampon riveraine globale et section). Les relations entre la richesse des poissons dans le bassin versant, les valeurs d'IBI et les variables prédictives du paysage sont les plus fortes à l'échelle de la zone riveraine et la variable explicative la plus forte est la forêt riveraine ($r^2 = 0{,}63$, $P < 0{,}01$). L'analyse par ordination NMS révèle des similarités claires entre les peuplements de poissons des bassins dominés par l'agriculture et les peuplements retrouvés dans les petits cours d'eau d'amont. De même, les bassins versants forestiers et les bassins de plus grande surface possèdent des peuplements de poissons semblables. Nos résultats indiquent que tant les peuplements de poissons locaux que régionaux sont structurés par des caractéristiques du paysage à plus grande échelle; la couverture des terres fournit une meilleure indication du volume d'habitat disponible que ne le font la surface du bassin versant et l'ordre du cours d'eau.

[Traduit par la Rédaction]

## Introduction

There is much need to understand how human alterations in catchments affect stream communities. Because broad-scale, land use based planning and conservation efforts are often difficult to implement, an understanding of the relationships between biota and landscape characteristics is essential so as to effectively target management efforts. However, it is likely that the appropriate scale (local, regional, or whole catchment) at which to focus land use based stream conservation efforts is dependent on ecosystem character (Johnson and Covich 1997). Here we examine the relative influence of local vs. regional landscape factors in regulating fish assemblages in an ecoregion of the northern Great Plains.

With reference to their surrounding landscapes, stream fish assemblages are structured by in-stream habitat condition (Orth 1983; Rahel and Hubert 1991) and by interaction with the surrounding terrestrial landscape (Roth et al. 1996; Wang et al. 1997; Snyder et al. 2003). Anthropogenic alteration of in-stream habitats often has direct negative impacts on fish assemblage health (Gorman and Karr 1978; Fausch and Northcote 1992), whereas alteration of the surrounding terrestrial landscape impacts stream systems through mechanisms such as in-stream sedimentation, hydrologic alteration, reduced

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woody debris inputs, reduced shading, and nutrient enrichment (Allan 2004). Spatially, riparian (near-stream) landscape characteristics (Johnson and Covich 1997; Naiman and Decamps 1997), intermediate-scale characteristics (Burnett et al. 2006), and catchment-wide characteristics (Cronan et al. 1999; Peterson and Kwak 1999; Castillo et al. 2000) all have been identified as important regulators of stream processes.

In many regions, catchment-level land cover alterations have been identified as having greater negative influence on fish assemblages than reach or riparian alterations (Allan et al. 1997; Wang et al. 1997; Harding et al. 1998). In contrast, in streams characterised by low anthropogenic landscape change, local habitat scale variables are usually the best predictors of patterns of fish occurrence, abundance, and assemblage composition (Wang et al. 2003). However, even in studies of anthropogenically altered environments, reach riparian characteristics can act as better predictors of fish assemblage composition than catchment-level factors (Stauffer et al. 2000; Meador and Goldstein 2003). As such, comparing among-scale landscape relationships can be an effective means of identifying potential processes most linked to in-stream factors (Burnett et al. 2006).

Fish assemblages in prairie ecosystems offer an excellent opportunity to examine the role of landscape parameters in regulating community structure. Prairie streams are characterized by high natural levels of hydrologic disturbances such as drought and flooding (Dodds et al. 2004). In these streams, variation in local environmental conditions including discharge, temperature fluctuation, turbidity, and salinity act to shape stream fish assemblage structure (Matthews 1987). In the Kansas River basin, broad-scale soil and stream size indicators were important predictors of fish assemblages, with local habitat measurements providing little extra predictive ability (Gido et al. 2006). Both water clarity and salinity (Taylor et al. 1993; Higgins and Wilde 2005) have been implicated as important factors shaping fish assemblages in Prairie regions. Fish species persisting in this environment must be able to tolerate or quickly recover from disturbance (Matthews 1987). As such, the existence of suitable refugia during times of drought and the ability to move between suitable habitat patches is of particular importance.

Over an evolutionary time scale, fish assemblages of the Great Plains have been shaped by major geomorphic and climatic changes, species dispersal abilities, and species tolerance levels (Hoagstrom and Berry 2006). As a result of these historical influences, fish communities in the northern Great Plains have low species richness and are largely dominated by tolerant species. How landscape across multiple spatial scales influences fish assemblage structure in the northern Great Plains remains largely unstudied. The Aspen Parkland Ecoregion is a grassland ecoregion interspersed with forest and covers much of the transition between the Northern Great Plains Boreal Forest (Ricketts et al. 1999). Because of the naturally high levels of hydrologic disturbance, largely tolerant species assemblages, and historically forested riparian areas of the Aspen Parkland Ecoregion, we predict that fish assemblage structure will be more strongly influenced by local habitat and riparian character than by more broad-scale landscape characteristics.

Here we examined the relative influence of local vs. regional landscape factors in shaping fish assemblages of the Aspen Parkland Ecoregion of the northern Great Plains. We compared fish assemblage structure with catchment land cover characteristics at two scales: overall catchment (total area draining to an outlet point) and overall riparian (all land within 150 m of a stream network). We then compared the relationships of fish assemblage structure with land cover and habitat characteristics in a set of subcatchments from within these catchments using three landscape scales: overall subcatchment (total area draining to an outlet point upstream of a catchment outlet), overall riparian (all land within 150 m of a subcatchment stream network), and reach habitat (along a segment of the stream network) (Fig. 1). By examining similarities and differences in the relationships between landscape and fish assemblage structure across multiple scales, our study is meant to improve our understanding of how fishes within the region are influenced by the surrounding landscape and to identify potential processes driving these responses.

## Materials and methods

### Study area

We conducted this analysis in the Aspen Parkland Ecoregion (Ricketts et al. 1999) of Manitoba, Canada (Fig. 2). This ecoregion was historically characterised by upland vegetation of interspersed grassland and broadleaf – mixed wood forest with riparian zones being dominated by mainly deciduous forests. Two other closely associated ecoregions, the Boreal Transition and Selwyn Lake Uplands ecoregions, intersperse the larger Aspen Parkland. The headwaters of a number of streams included in this study originate these areas of generally higher elevation.

Over the past century, most of the grasslands and many of the forests that once characterised the Aspen Parkland have been converted to agricultural use or pasture but little urban development has occurred, and it is estimated that only 10% of the ecoregion's natural habitats remain intact (Ricketts et al. 1999). Most cropland in the region is dedicated to the production of grain or oilseeds, and in 2001, between 40% and 50% of cropland acres in the region were managed under low-tillage or no-tillage systems (Statistics Canada 2001).

### Data collection and catchment selection

Fish assemblage and local habitat data for the region were obtained from Fisheries and Oceans Canada (DFO), which carried out sampling on 207 wadeable streams in the region between 2002 and 2004 as part of the Fish Habitat Inventory of Agro-Manitoba (Milani 2006). Sampling of sites was conducted by DFO staff between June and August with procedures used varying based on site character: either seining or backpack electroshocking methods were applied to sample fish in all representative habitats at a site.

Based on the distribution of stream sites sampled by DFO, 37 large 4th- and 5th-order regional catchments covering a cumulative area of 18 034 km$^2$ (Fig. 2) were selected for further analysis using the following criteria: (*i*) freely available land cover data for the entire catchment; (*ii*) the fish assemblage must have been sampled at least once at the streams highest order and once at a lesser order; and (*iii*) no extensive upstream channel modification. In our catchment-scale fish assemblage analysis, only total

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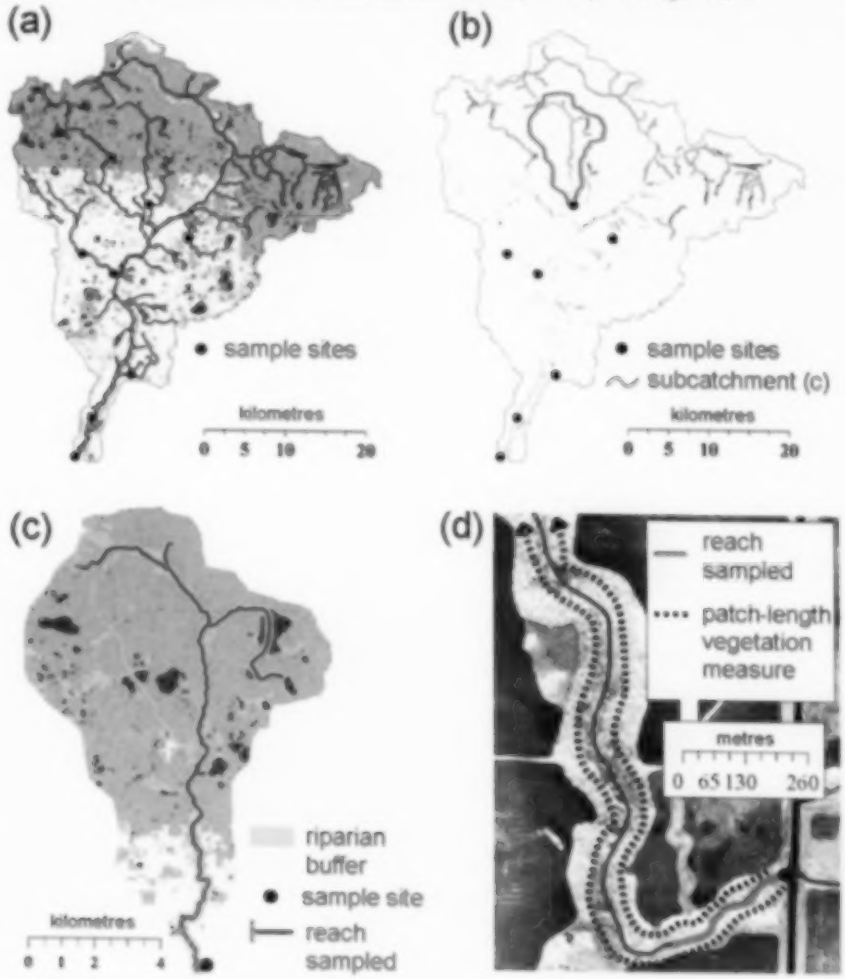
**Fig. 1.** Scales of landscape examined during this study: (*a*) entire catchment; (*b*) 150 m riparian buffer and the subcatchment; (*c*) entire subcatchment, overall 150 m riparian buffer; and (*d*) sampled reach and vegetated patch length reach.




richness and presence or absence data were used so as to reduce potential bias associated with varying sampling methodology.

From within these catchments, 48 subcatchment sites were selected for analysis to examine patterns of fish assemblage character at intermediate and finer scales. These sites were selected to meet the assumption of a consistent fish assemblage sampling method. At each site, an effort was made to sample all habitat types present, but sites were only included if they had been sampled over a reach of at least 15 × stream width by backpack electrofishing (Niemela et al. 1999). Sites located near a stream's confluence with a much larger river or a reservoir were excluded from analysis to avoid elevated richness measures associated with sampling the larger regional species pool (Fausch et al. 1984). Sites were excluded if they were located within 3 km of a stream's confluence with a river greater than two stream orders or within 3 km upstream or downstream of a major reservoir. In addition, only sites with upstream catchments less than 450 km$^2$ in size were selected to reduce the amount of overlap in size between catchments and subcatchments.

To test for potential spatial autocorrelation of our data sets, Pearson's correlation was applied first at the catchment scale for the distance between sites and difference between richness scores for those sites and then at the subcatchment scale for the distance between sites and the difference between IBI scores. Neither relationship was significant ($P > 0.05$), so the data at these scales were accepted as independent.

To evaluate reach habitat conditions at each site, a visual habitat assessment was completed over a distance of at least 15 × stream width using 12 habitat variables selected by DFO: epifaunal substrate, embeddedness, velocity – depth regime, sedimentation, channel flow status, channelization, frequency of riffles or bends, bank stability, vegetative protection, riparian vegetative width, pool substrate, and pool variability. This assessment was based on the visual habitat assessment protocol defined by the US Environmental Pro-

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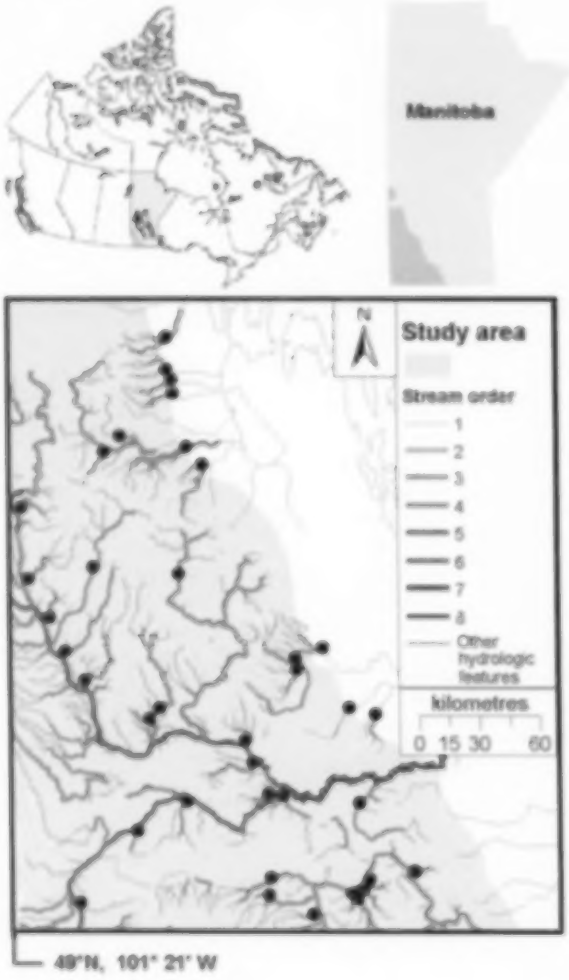


**Fig. 2.** Southwestern Manitoba streams in the Aspen Parkland and associated ecoregions. Solid circles indicate outlets of study catchments.

tection Agency for rapid bioassessment of wadeable streams (Barbour et al. 1999).

### Land cover

All landscape variables were determined from existing electronic databases using ArcMap 9.0 software (Environmental Systems Resource Institute (ESRI) 2004). Sampling site geographic coordinates were verified, and stream orders were determined by overlaying site location on digital stream network maps available through the Manitoba Conservation Land Information Division (2004). Catchments upstream of defined outlets or subcatchments upstream of point sample sites meeting the criteria outlined for inclusion in analysis were delineated using a 1:50 000, 30 m pixel resolution digital elevation model (DEM) from DMTI Spatial Inc. (2002). These boundaries were verified by comparing catchment boundaries with those shared with catchments delineated in the Incremental Gross Drainage Areas of the PFRA Watershed Project (Prairie Farm Rehabilitation Administration (PFRA) 2005). The boundaries defined were then used to summarize landscape attributes.

For all catchments and subcatchments analysed, average catchment slope was calculated as the average elevation rise over horizontal run between neighbouring cells in the DEM. Land cover was defined using 16-category, 30 m pixel resolution Landsat 7 Thematic Mapper (TM) maps from 1994 (Manitoba Conservation Department and Manitoba Remote Sensing Centre 1994). For catchments with headwaters originating in North Dakota, Landsat 7 imagery with the same 30 m pixel resolution originating from the USGS National Prairie Wildlife Centre (Strong et al. 2004) were combined with data from the province of Manitoba by summarizing land cover classes into the same 16 categories used by the province of Manitoba.

Eight of the 16 land use – cover categories (cultural, forage crop, forest cutblock, burns, treed rock, bogs, open gravel, and unclassified) included in the Manitoba Conservation Landsat TM maps comprised less than 1% of the area of any catchment or subcatchment and were excluded from analysis. Forest categories besides deciduous forest were present in relatively small proportions in most catchments and so all forest types were pooled to create one forest category accounting for all woody vegetation. The final categories used in analysis were agriculture, grassland, forest, open water, and marsh. In all catchments, these categories comprised at least 95% of catchment land cover.

#### *Catchments*

Catchment land cover was defined at two broad spatial scales: for the entire catchment and for the entire riparian buffer within 150 m of the stream network.

#### *Subcatchments*

Subcatchment land cover was defined upstream of selected sampling sites at two broad spatial scales: overall subcatchment land cover and overall 150 m riparian buffer land cover. In addition, two finer scales were examined: patch length and reach habitat. Total patch length of woody riparian vegetation was defined as the total length both upstream and downstream from a sampled reach greater than 50 m in width, without anthropogenic disturbance (roads or agriculture) over a length of more than 50 m on either bank. This metric was manually measured using black and white aerial photographs from Manitoba Conservation and Linnet Geomatics International Inc. (1998). Habitat characteristics were defined through the habitat assessments conducted by DFO.

Because landscape variables across multiple spatial scales are not independent, Pearson's correlations were used to examine the relationships between landscape variables for each of the landscape scales considered.

### Data analysis

#### *Fish and landscape relationships among catchments*

Because the catchments examined were quite large (4th and 5th order), we summarized data into fish species presence or absence. In addition, a value for total regional richness was examined representing all species occurring in the catchment (excluding nonreproducing stocked species). Regression analyses were used to examine the relationships be-

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**Table 1.** Metrics used in the calculation of index of biotic integrity (IBI) scores were assigned a value of 1, 3, or 5 for a maximum possible total of 60, with scoring based on Niemela et al. (1999).

| Metric | Comments |
|---|---|
| Total number of species | Scoring varies with drainage area |
| Evenness | |
| Number of minnow species | Scoring varies with drainage area |
| Percent pioneer individuals | Scoring varies with drainage area |
| Percent headwater individuals | |
| Number of benthic insectivores species | |
| Percent piscivore individuals | |
| Percent omnivore individuals | Percent individuals used rather than biomass* |
| Percent insectivore individuals | Percent individuals used rather than biomass* |
| Percent simple lithophilic spawners | |
| Percent tolerant individuals | |
| Number of sensitive species | Scored based on drainage area |
| Number of individuals per metre | Scoring varies with drainage area |
| Percent with deformities, eroded fins, lesions, tumours | |

*Indicates modification from Niemela et al. (1999).

tween species richness and land cover. Land cover proportions were arcsine (square root) transformed to achieve normality. Because landscape variables are represented as a proportion of the entire catchment, they are not independent of one another. Therefore, presenting our results in this form is meant to provide a descriptive indication of the strengths of the relationships examined (Roth et al. 1996; Snyder et al. 2003). Regression and correlation analyses were performed using JMP software (SAS Institute Inc. 2001).

Nonmetric multidimensional scaling (NMS) ordination was used to investigate which landscape variables were significantly correlated with fish assemblage data sets and to identify patterns of species association among catchments. NMS ordination is based on ranked distance order of similarity between samples. It is well suited to the analysis of ecological data because it assumes no underlying distribution of the data used and is able to deal with data containing many zero values for species (McCune and Grace 2002). A Sorenson (Bray–Curtis) distance measure was selected as it assumes no underlying distribution of the data (McCune and Grace 2002). A random time of day starting configuration was used with 40 runs with real data and 400 runs with randomized data. All solutions were run until the standard deviation in stress over the last 10 iterations was less than 0.001. We ran Monte Carlo tests for all ordinations to identify the number of dimensions beyond which stress was not significantly reduced so as to determine the appropriate number of dimensions in which to run each test. For all tests, a three-dimensional solution was identified as most suitable, exhibiting the lowest possible stress value with $P < 0.05$. To identify which variables to incorporate into a final model, two preliminary ordinations were run, both with species as the main matrix but differing in that the second matrix was composed of overall catchment or overall riparian buffer variables, respectively. From each of these ordinations, the five strongest landscape predictors were selected for inclusion in a final ordination based on $r^2$ values. Only fish species that occurred in at least 5% of the catchments were used in ordination to prevent the introduction of bias or the overestimation of minor patterns in assemblage composition. All ordination analyses were performed using PC-ORD (McCune and Mefford 1999).

### *Fish assemblage and landscape relationships among subcatchments*

For subcatchment assemblage analysis, data were again summarized as presence or absence and total richness was calculated. In addition, an index of biotic integrity (IBI) scores was calculated for each catchment as an indicator of assemblage integrity (Table 1). We used the criteria outlined by Niemela et al. (1999) for the Red River Basin in the Lake Agassiz Plain Ecoregion, which is located directly to the southeast and is within the same drainage basin (Hudson's Bay) as the Aspen Parkland of Manitoba. Because all species collected during this study were also sampled by Niemela et al. (1999) in the Lake Agassiz Plain Ecoregion, the index was deemed suitable; however, a number of modifications were made owing to the nature of the available fish assemblage data sets and slight variations in ecoregional assemblage structure. Percent omnivorous individuals and percent insectivorous individuals were used rather than percent biomass, because data for individual specimen sizes were not available. Potential scores for the resulting index ranged from 0 to 60, with 0 representing the poorest possible and 60 representing the best possible assemblage integrity.

The relative strength of landscape–richness and landscape–IBI relationships for between subcatchments was examined using regression analyses. NMS ordination was applied to this data set to examine landscape correlations with the fish assemblage data set (presence or absence). Two primary NMS ordinations were performed correlating this matrix with overall landscape variables and with reach variables following the same methods as for the overall catchment scale. From these ordinations, the five strongest landscape predictors and four strongest habitat predictors were selected for inclusion in a final ordination based on $r^2$ values.

## Results

### Landscape and habitat character

Land cover in both major study scales (catchment and subcatchment) varied considerably (Table 2). Catchments averaged 474 km$^2$ (131–1856 km$^2$) in size and varied con-

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**Table 2.** Mean, standard error (SE), and range for catchment landscape ($n$ = 37), subcatchment landscape ($n$ = 48), and selected reach variables.

| | Catchments | | Subcatchments | |
|---|---|---|---|---|
| Landscape variable | Mean ± SE | Range | Mean ± SE | Range |
| 150 m riparian agriculture (%) | 42.1±3.0 | 3.2–67.7 | 24.9±3.5 | 0–80.3 |
| 150 m riparian grassland (%) | 25.9±1.2 | 6.1–36.5 | 19.8±2.1 | 0–51.3 |
| 150 m riparian open water (%) | 2.3±0.4 | 0.0–13.2 | 3.8±1.3 | 0–57.8 |
| 150 m riparian marsh (%) | 5.1±0.9 | 0.3–23.5 | 9.2±1.3 | 0–31.5 |
| 150 m riparian forest (%) | 20.6±3.1 | 0.1–62.7 | 39.3±4.1 | 0–92.2 |
| Agriculture (%) | 54.7±3.8 | 9.5–83.9 | 33.6±4.3 | 0.1–87.3 |
| Grassland (%) | 16.2±0.9 | 3.2–25.7 | 15.3±1.8 | 0.1–48.4 |
| Open water (%) | 1.2±0.3 | 0.0–10.1 | 2.3±0.6 | 0–19.7 |
| Marsh (%) | 4.2±0.4 | 0.4–13.7 | 5.2±0.6 | 0.3–17.8 |
| Forest (%) | 19.0±3.4 | 0.2–64.3 | 39.9±4.5 | 0.1–93.1 |
| Slope (%) | 0.83±0.06 | 0.32–1.53 | 1.24±0.10 | 0.07–2.73 |
| Area (km$^2$) | 474.7±60.0 | 151.4–1856 | 154.5±19.0 | 4.4–570.1 |
| Patch length (km) | — | — | 3.46±0.58 | 0–10 |
| Conductivity (μmhos) | — | — | 573.6±29.9 | 273–1129 |
| Turbidity (NTU) | — | — | 6.1±1.0 | 0.42.41 |
| Epifaunal substrate* | — | — | 13.9±0.5 | 4–18 |
| Frequency of riffles or bends* | — | — | 12.8±0.6 | 5–19 |
| Vegetative protection* | — | — | 14.0±0.6 | 4–20 |
| Habitat score* | — | — | 128.1±3.4 | 64–181 |

*Indicates categorically assigned habitat variable, actual scores were whole numbers ranging from 1 to 20. Total habitat scores ranged from 10 to 200.

siderably in terms of land cover, most notably with proportion of agriculture ranging from 9.5% to 83.9% in the entire catchment and from 3.2% to 67.7% within the overall 150 m riparian area. Subcatchments averaged 144 km$^2$ (14–450 km$^2$) in size, with total agricultural land cover varying from 0.1% to 87.3% and overall 150 m riparian agriculture values varying from 0% to 80.3%. For both the catchment and subcatchment scales, slope exhibited a strong negative correlation with percent agriculture ($r$ = –0.80, $P < 0.01$, and $r$ = –0.77, $P < 0.01$, respectively) and a strong positive correlation with percent forest ($r$ = 0.80, $P < 0.01$, and $r$ = 0.71, $P < 0.01$, respectively). Grassland was also an important landscape component in many catchments, generally exhibiting a negative relationship with forest and marsh land covers, especially within the riparian zone ($r$ = –0.62 and –0.73, respectively, $P < 0.01$).

Local reach habitat quality scores for subcatchments varied from 64 to 181 and correlated with both forest (+) and agriculture (–) land cover categories. Correlations between habitat scores and land uses were generally strongest between overall subcatchment agricultural ($r$ = –0.56, $P < 0.01$) and forest ($r$ = 0.52, $P < 0.01$) categories, with riparian versions of the same land cover variables being slightly less correlated ($r$ = –0.51, $P < 0.01$, and $r$ = 0.43, $P < 0.01$, respectively). Riparian patch length varied from 0 to 10 km but did not correlate well with any other landscape factors, although a general positive trend was illustrated with overall forested land cover ($r$ = 0.38) and overall riparian marsh ($r$ = 0.41), but neither trend was statistically significant ($P > 0.05$).

### Fish assemblages

Twenty-five fish species were collected across the study region. Total catchment regional richness values varied from 0 to 14 species, whereas the richness in subcatchments ranged from 1 to 11 species. The most commonly occurring species in the study catchments were white sucker (*Catostomus commersoni*) and fathead minnow (*Pimephales promelas*), both sampled in 86% of catchments, and the creek chub (*Semotilus atromaculatus*) (73%).

For subcatchments, species of the family Cyprinidae comprised on average 58% of total species richness. The most common species in terms of the proportion of sites present were again *Catostomus commersoni* (69%) and *Pimephales promelas* (60%), in addition to the western blacknose dace (*Rhinichthys obtusus*) (64%).

IBI scores ranged from 14 (very poor) to 44 (good) out of a possible 60. Based on the species classifications outlined by Niemela et al. (1999), tolerant species comprised on average 76% of the total number of individuals caught at sites. When separated by feeding guild, insectivorous fish comprised on average 50% of individuals sampled, whereas omnivores comprised on average 30%. Although larval piscivores were sampled in a number of catchments in the region, adult piscivores were not sampled at any of the subcatchments meeting the assumptions needed for inclusion in our analysis.

### *Catchment fish assemblage structure – landscape relationships*

Land cover characteristics show clear separations across both axes 1 and 3 (Fig. 3; Table 3). A negative association is exhibited between agricultural land covers and all other land covers, with the exception of a weak positive association with riparian grassland (Fig. 3; Table 3). Landscape variables were able to explain a large portion of the variance in fish assemblage structure. At the catchment scale, the final

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**Fig. 3.** Nonmetric multidimensional scaling (NMS) plots of fish assemblages in the Aspen Parkland Ecoregion of Manitoba for (*a*) catchment-scale fish assemblage structure and (*b*) subcatchment-scale fish assemblage structure. Only those land cover variables with $r^2 > 0.15$ are plotted. Final stress for ordination: (*a*) 15.14, (*b*) 13.65. Fish species codes as in Table 4. Variable codes as in Table 3.

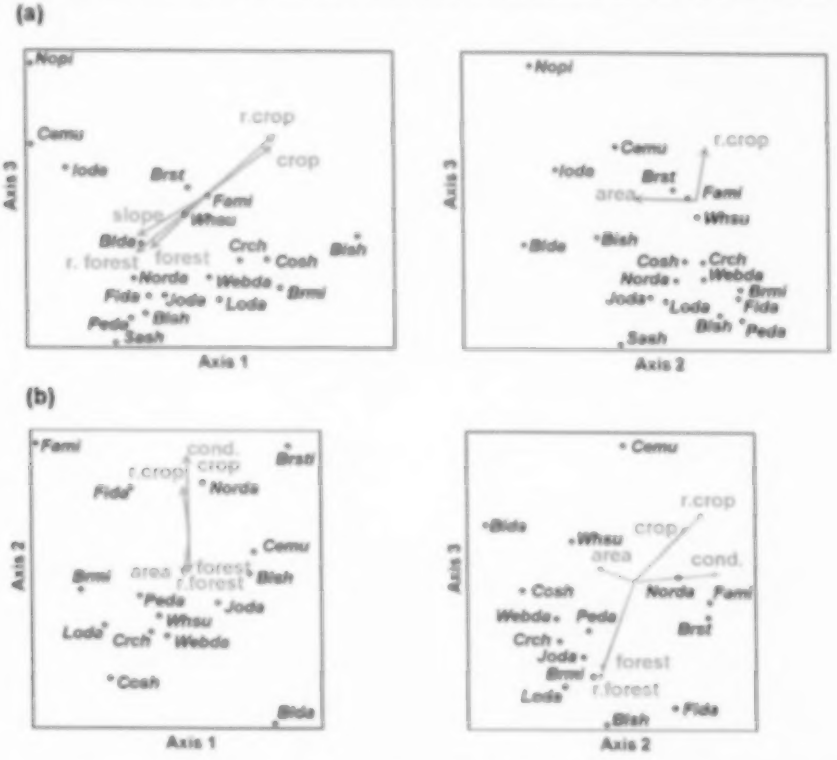


**Table 3.** Correlation coefficients ($r$) of landscape and habitat variables with the resultant ordination axes for each of the catchment- and subcatchment-scale nonmetric multidimensional scaling (NMS) of fish assemblage data.

| | Catchment ordination: correlation with NMS axis | | | | Subcatchment ordination: correlation with NMS axis | | |
|---|---|---|---|---|---|---|---|
| Variable (code) | 1 | 2 | 3 | Variable (code) | 1 | 2 | 3 |
| Cropland (crop) | 0.408 | 0.098 | 0.354 | Cropland (crop) | –0.106 | 0.308 | 0.317 |
| Forest (forest) | –0.364 | –0.099 | –0.352 | Forest (forest) | 0.034 | –0.243 | –0.397 |
| Area (area) | –0.371 | –0.422 | 0.071 | Area (area) | –0.095 | –0.263 | 0.16 |
| Slope (slope) | –0.399 | –0.16 | –0.308 | 150 m riparian cropland (r.crop) | –0.068 | 0.35 | 0.352 |
| 150 m riparian cropland (r.crop) | 0.418 | 0.17 | 0.391 | 150 m riparian forest (r.forest) | 0.035 | –0.25 | –0.422 |
| 150 m riparian forest (r.forest) | –0.404 | –0.098 | –0.367 | Conductivity (cond.) | –0.05 | 0.39 | 0.118 |
| Grassland | –0.382 | 0.014 | –0.091 | Frequency of riffles–bends | –0.134 | –0.172 | –0.157 |
| 150 m riparian grassland | 0.202 | –0.048 | 0.12 | Epiphaunal substrate | –0.152 | –0.01 | –0.148 |
| 150 m riparian water | –0.158 | –0.32 | –0.149 | Habitat score | –0.15 | 0.089 | –0.154 |
| 150 m riparian marsh | 0.141 | 0.06 | –0.19 | | | | |

three-dimensional NMS ordination was able to explain most of the variation in fish assemblage structure (88.4%; Table 4). There is a clear separation of fish species across the gradient from high to low cropland, although at the catchment scale, almost all species exhibit some negative correlation with cropland covers. In addition, catchment area and headwater–nonheadwater species separate across axes 1 and 2 (Fig. 3; Table 4).

### *Subcatchment fish assemblage structure – landscape relationships*

For subcatchments, three NMS axes were able to explain 82% of the variation observed in fish assemblage structure (Fig. 3; Table 4). At the local catchment scale, land cover relationships show essentially the same patterns as at the regional catchment scale. Cropland land cover separates from noncropland covers across axes 2 and 3 (Fig. 3; Table 3).

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**Table 4.** Correlation coefficients ($r$) of fish species with the resultant ordination axes for each of the catchment- and subcatchment-scale nonmetric NMS of fish assemblage data.

| | Catchment ordination: correlation with NMS axis | | | Subcatchment ordination: correlation with NMS axis | | |
|---|---|---|---|---|---|---|
| Species (code) | 1 | 2 | 3 | 1 | 2 | 3 |
| *Catostomus commersoni* (Whsu) | –0.456 | 0.031 | –0.325 | –0.267 | –0.585 | 0.442 |
| *Culaea inconstans* (Brst) | –0.259 | –0.389 | 0.126 | 0.616 | 0.491 | –0.280 |
| *Etheostoma nigrum* (Joda) | –0.329 | –0.387 | –0.618 | 0.136 | –0.265 | –0.456 |
| *Luxilus cornutus* (Cosh) | 0.681 | –0.123 | –0.493 | –0.256 | –0.388 | –0.04 |
| *Margariscus margarita* (Peda) | –0.356 | 0.217 | –0.441 | –0.159 | –0.159 | –0.2 |
| *Notropis heterolepis* (Blsh) | –0.266 | 0.102 | –0.393 | 0.16 | –0.08 | –0.478 |
| *Percina maculata* (Blda) | –0.242 | –0.656 | –0.132 | 0.171 | –0.321 | 0.142 |
| *Phoxinus eos* (Norda) | –0.245 | –0.072 | –0.213 | 0.031 | 0.106 | 0.011 |
| *Phoxinus neogaeus* (Fida) | –0.391 | 0.29 | –0.524 | –0.22 | 0.164 | –0.606 |
| *Pimephales promelas* (Fami) | 0.119 | –0.209 | 0.035 | –0.588 | 0.315 | –0.102 |
| *Rhinichthys cataractae* (Loda) | 0.081 | –0.162 | –0.4 | –0.19 | –0.168 | –0.296 |
| *Rhinichthys obtusus* (Webda) | 0.065 | 0.085 | –0.726 | –0.177 | –0.67 | –0.376 |
| *Semotilus atromaculatus* (Crch) | 0.518 | 0.093 | –0.664 | –0.2 | –0.421 | –0.392 |
| *Umbra limi* (Cemu) | –0.543 | –0.251 | 0.125 | 0.171 | –0.03 | 0.453 |
| *Etheostoma exile* (Ioda) | –0.383 | –0.385 | 0.061 | — | — | — |
| *Hybognathus hankinsoni* (Bemi) | 0.242 | 0.136 | –0.212 | — | — | — |
| *Notropis dorsalis* (Bish) | 0.488 | –0.31 | –0.09 | — | — | — |
| *Notropis stramineus* (Sash) | –0.279 | –0.237 | –0.343 | — | — | — |
| *Esox lucius* (Nopi) | –0.479 | –0.452 | 0.276 | — | — | — |

**Note:** Rare species occurring in fewer than 5% of study catchments or subcatchments, respectively, were not included in ordination analysis. Dash (—) indicates species occurring in less than 5% of study subcatchments.

**Table 5.** Regression coefficients ($r^2$) for fish assemblage variables and landscape at the subcatchment and entire catchment scales.

| | Catchment | Subcatchment | |
|---|---|---|---|
| Landscape variable | Richness | Richness | IBI |
| 150 m riparian cropland | –0.470 | –0.161 | –0.507 |
| 150 m riparian grass | — | — | –0.147 |
| 150 m riparian marsh | 0.247 | 0.123 | 0.171 |
| 150 m riparian forest | 0.630 | 0.161 | 0.525 |
| Cropland | –0.425 | –0.109 | –0.368 |
| Marsh | — | 0.142 | — |
| Forest | 0.59 | 0.133 | 0.389 |
| Area | — | — | — |
| Slope | 0.388 | — | 0.339 |
| Patch length | — | 0.106 | 0.13 |
| Regional richness | — | 0.101 | 0.305 |
| Habitat score | — | — | 0.285 |
| Epiphaunal substrate | — | 0.114 | 0.221 |
| Vegetative protection | — | — | 0.24 |

**Note:** Only significant results ($P < 0.05$) are given; dash (—) indicates results not significant.

Reach-scale habitat variables did not show obvious correlations with any axis, except for site conductivity, which showed a positive association with cropland (Table 3).

Subcatchment area explained some variation in species structure but to a lesser extent than the analysis we conducted at the catchment scale (Fig. 3; Tables 3, 4). Generally we found that more-tolerant species (e.g., *Pimephales promelas*, *Culaea inconstans* (brook stickleback), *Umbra limi* (central mudminnow), and *Phoxinus eos* (northern redbelly dace)) were associated across either axis 2 or axis 3 (Fig. 3; Table 4). Most other fish species were more strongly associated with natural, forested land covers.

### *Catchment fish assemblage richness – landscape relationships*

We found a strong positive relationship between forest cover and species richness at the regional catchment scale for both the entire catchment and the riparian area, whereas the opposite relationship was true of agricultural cover (Table 5). All relationships between fish richness and landscape predictors were strongest at the riparian scale, with the strongest single predictor being riparian forest ($r^2 = 0.63$, $P < 0.01$). Species richness increases rapidly with the percentage riparian forest cover to about 20%, followed by a gradual increase to the maximum proportion riparian forest cover observed (Fig. 4). The opposite trend is observed when fish species richness is plotted with riparian agricultural cover. There is a sharp decline in species richness after a threshold of 40% riparian agriculture in the catchment (Fig. 4). No other variable explained a significant proportion of the residual variation from these relationships.

### *Subcatchment fish assemblage richness, biotic integrity – landscape relationships*

Relationships between fish richness and landscape predictors for local catchments were weaker than for regional catchments. No land cover or habitat variable was able to explain more than 16% of the observed variation in richness (Table 5), and no variable was able to explain more than 1% of the residual variation. Interestingly, only weak relationships existed between local catchment richness and surrounding regional catchment richness, indicating that factors other than those observed in this study control local rich-

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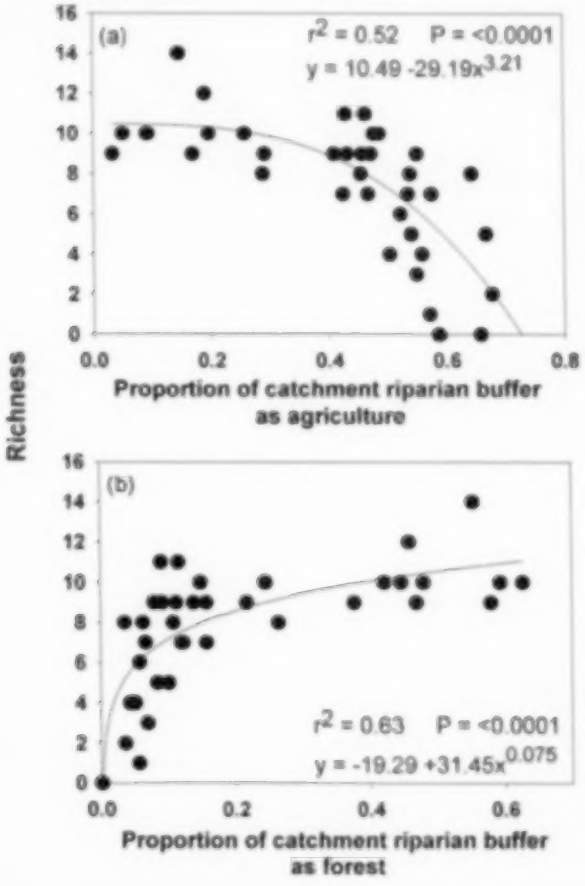
(a)
$r^2$ = 0.52 P = <0.0001
y = 10.49 -29.19x$^{3.21}$
Richness
Proportion of catchment riparian buffer as agriculture
(b)
$r^2$ = 0.63 P = <0.0001
y = -19.29 +31.45x$^{0.075}$
Proportion of catchment riparian buffer as forest

**Fig. 4.** Relationship of regional catchment richness to (*a*) riparian cropland and (*b*) riparian forest in the Aspen Parkland Ecoregion of Manitoba.

ness. Similarly, when Shannon's diversity (*H'*) was calculated for point sample assemblages, all variables explained less than 10% the observed variation, with the exception of the epiphaunal substrate habitat ($r^2$ = 0.23, $P < 0.05$).

We found strong linear relationships between landscape variables and local IBI scores (Fig. 5; Table 5). These relationships were strongest at the riparian scale. At the riparian scale, IBI scores were best predicted by the proportion of overall 150 m riparian forest cover ($r^2$ = 0.53, $P < 0.01$) and with riparian agricultural cover ($r^2$ = –0.51, $P < 0.01$). No other catchment, landscape, or habitat variable was able to explain more than 4% of the residual variation. Of the habitat metrics observed, only total habitat, epiphaunal substrate, and vegetative protection scores explained more than 10% of IBI score variation (Table 5). These same variables, however, showed relatively strong negative correlations with agricultural land cover and positive correlations with forested land cover (not shown).

## Discussion

Our findings indicate that in the Aspen Parkland Ecoregion, fish assemblage health (as measured by catchment richness and local reach biotic integrity indices) is best predicted by land cover throughout the overall catchment or subcatchment riparian zone. Our results add support to the argument that broader spatial scales, rather than local reach characteristics, need to be considered to effectively maintain healthy fish assemblages.

For subcatchments, reach habitat scores were strongly correlated with landscape variables; however, reach habitat metrics were relatively poor predictors of fish assemblage health in comparison to landscape variables measured at broader scales. This pattern may be related to a relatively wide range of agricultural land cover in our study, which reduces our ability to detect an effect of local habitat quality. However, because the range of habitat quality that we found was also very variable, it seems likely that local fish assemblage health may be more strongly related to regional habitat and fish patterns rather than local habitat patch quality. Others have found that entire catchment land cover tends to overshadow riparian land cover in terms of its role in affecting fish assemblage structure (Allan et al. 1997; Wang et al. 1997; Harding et al. 1998). Our study indicates that overall riparian land cover can serve as a better predictor of fish assemblages. Thus the influence of land cover on fish assemblages likely varies by region such that no one spatial scale is likely to be identified universally as a best predictor for all stream systems.

Forest and agricultural land cover were strongly correlated across spatial scales. As such, it is difficult to assess whether the relationships with fish that we found resulted directly from negative agricultural land cover impacts or are simply related to a reduction in riparian forest associated with increased cropland. Although forested riparian zones reduce nutrient inputs and improve habitat conditions in agricultural catchments, fish assemblages were found to be unaffected by the presence or absence of riparian areas in Michigan streams (Moerke and Lamberti 2006). In our study, only one of the local-scale catchments included in this analysis exhibited a high level of entire catchment agriculture while maintaining a high proportion of riparian area as forest (Fig. 6). This site also had the highest IBI score (44), indicating that relatively healthy fish assemblages can exist in highly agricultural catchments as long as a high proportion of the catchment's riparian area remains forested.

Overall, our study provides evidence that the health of riparian areas is likely important in shaping fish assemblages in the northern Great Plains region where forested areas have historically composed a significant portion of the riparian landscape. Given that fish assemblage health has been shown to act as a strong indicator of overall stream ecosystem health (Karr 1981; Karr et al. 1985), our study, when examined in combination with similar work (e.g., Stauffer et al. 2000; Dodds and Oakes 2006), provides support for the argument that riparian areas likely offer an effective scale at which to focus stream conservation efforts in plains ecosystems.

### Mechanisms controlling landscape – assemblage structure relationships

Fish species structure within our catchments and subcatchments was also strongly structured by factors other than land cover. We found the fish community structure from larger catchments to be different than that from smaller-sized catchments. However, those species that were primarily found

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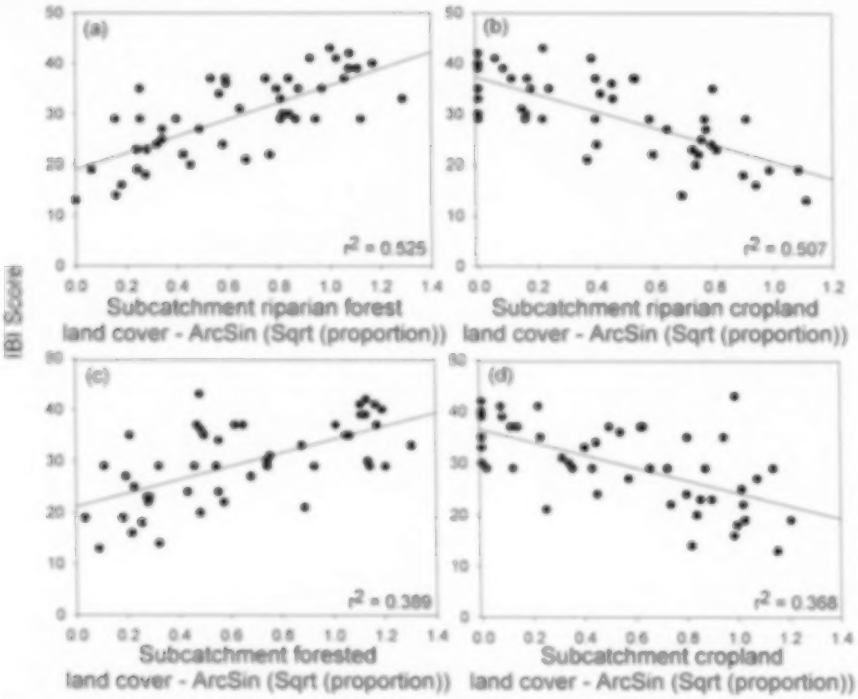
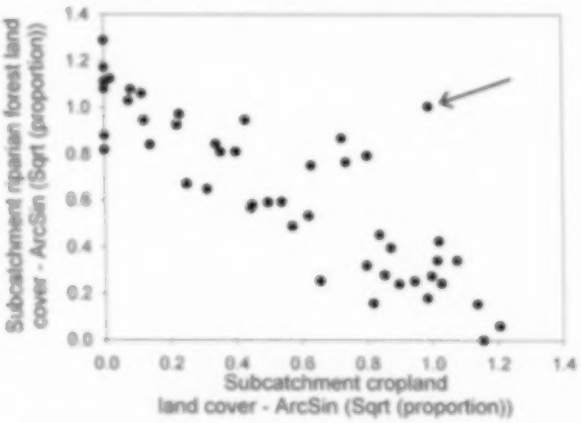
**Fig. 5.** Relationships between fish assemblage index of biotic integrity (IBI) scores and subcatchment (*a*) riparian forest, (*b*) riparian cropland, (*c*) total forest, and (*d*) total cropland in the Aspen Parkland Ecoregion of Manitoba. ArcSin (Sqrt (proportion)), proportion was arcsine (square root) transformed.




in smaller subcatchments were also positively related to greater cropland cover. Because no clear correlation existed between cropland cover and subcatchment area, this result may indicate that subcatchments with a greater proportion of cropland area show habitat characteristics similar to those of smaller subcatchments.

This pattern can be related to stream flow variability. Stream flow patterns have been shown to be significant predictors of fish assemblages, whereas species found in hydrologically variable streams are more generalists (Poff and Allan 1995). In particular, increased hydrologic variability reduces habitat volume in large catchments causing them to function and exhibit fish assemblage patterns similar to those in smaller headwater streams (Poff and Allan 1995). Fish assemblages are also affected in agricultural streams that exhibit increased flashiness of discharge, decreased low flow, and altered channel morphology (Infante et al. 2006). In our study, limited hydrological data were available for 23 of our study streams (collected through the Water Survey of Canada (2006)). We found no relationship between richness and annual or monthly discharge (not shown); however, a very strong negative relationship was exhibited between richness and the coefficient of variation (CV) for monthly discharge ($r^2$ = 0.72, $P < 0.01$) (Fig. 7). We also found a strong positive relationship between the CV of monthly discharge and overall riparian ($r^2$ = 0.53, $P < 0.01$), as well as whole-catchment agricultural land cover ($r^2$ = 0.49, $P < 0.01$). It appears that increased hydrologic variability and the resulting reduced habitat volume are likely mechanisms

**Fig. 6.** Relationship between subcatchment cropland land cover and subcatchment riparian forest cover in the Aspen Parkland ecoregion. The arrow indicates the subcatchment study site where a high proportion of the riparian zone remained as forest, but where catchment agriculture was high. ArcSin (Sqrt (proportion)), proportion was arcsine (square root) transformed.


Subcatchment riparian forest land cover - ArcSin (Sqrt (proportion))
Subcatchment cropland
land cover - ArcSin (Sqrt (proportion))

through which land cover controls the health of the fish assemblages within our study area.

In other regions, increased sediment inputs have also been implied as potential mechanisms through which land cover change affects fish assemblages (Roth et al. 1996; Allan

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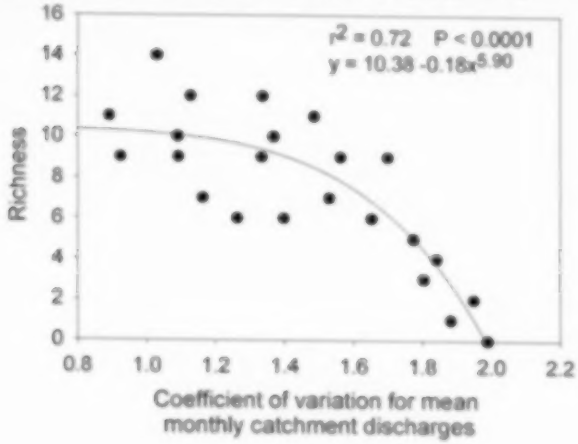
**Fig. 7.** Relationship between flow variability and species richness in catchments of the Aspen Parkland Ecoregion in Manitoba.




2004). However, sediment-related local habitat metrics and stream turbidity measures were poorly correlated with land cover variables and were not correlated with fish assemblage variables such as IBI scores and richness. Nevertheless, water quality represents a probable mechanism through which land cover affects the overall volume of suitable stream habitat for fish assemblages in our study area. Of particular importance may be salinity, which has been implicated as an important factor shaping stream fish assemblage structure in southern prairie regions (Higgins and Wilde 2005). Conductivity, which is strongly related to water salinity, has also been identified as an important variable in predicting fish assemblage structure in southern prairies (Taylor et al. 1993). In our study, conductivity was found to strongly correlate with agricultural land cover ($r = 0.71$, $p < 0.01$) and to be an important variable for fish in our ordination analysis.

We found no relationship between fish richness and area at both catchment and subcatchment scales. This is in contrast to several studies that have shown the existence of the logarithmic relationship in streams (Angermeier and Schlosser 1989; Changeux and Pont 1995; Xenopoulos et al. 2005). This lack of relationship could be attributed to large fluctuations in species richness resulting from the much greater environmental variability (e.g., floods, drought) in this region (Angermeier and Schlosser 1989). We did a find a strong logarithmic relationship at the broader catchment scale between forested land cover and fish richness. This relationship is much stronger for the overall riparian scale, indicating that riparian land cover is a better predictor of habitat space for fish than catchment area.

Most studies examining fish assemblage character in relation to land cover have used single-point measurements of fish assemblage and have focused on the subcatchment scale. To our knowledge, few other studies have pooled stream fish richness from multiple sites within catchments to examine between-catchment patterns in relation to land cover. This study suggests that examining catchment fish assemblages from multisite sampling points can add important information to multiscale landscape approaches.

In conclusion, both catchment and subcatchment fish and stream health were shown to be strongly affected by broader scales of landscape, with assemblage health driven primarily by overall catchment habitat quality. This dependence of local fish assemblage health on overall regional habitats indicates the importance for future work of considering the metapopulation dynamics of, connectivity of, and movements associated with seasonal habitat usage by fish assemblages in relation to the surrounding landscape. Even in a fish assemblage composed of largely tolerant and relatively habitat-plastic species, we illustrate a strong connection between assemblage composition and the surrounding terrestrial landscape. Our findings indicate that maintaining wooded riparian areas could be relatively effective in preventing the degradation of many stream fish assemblages, even in catchments with a relatively high proportion of agricultural upland land cover. It is possible that riparian conditions, which we observe to be strong predictors of fish assemblage structure, are the result of seasonal hydrological patterns, particularly of flashiness. Stream hydrology, in turn, is likely influenced by broader scales of land use. A more broad-scale approach needs to be adopted for riparian conservation to maintain healthy stream ecosystems. Whole-catchment riparian rather than reach riparian character and land use connections to hydrological variability are likely to provide a more effective scale of focus for future research, conservation, and monitoring efforts in similar regions.

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# Periphyton as an early indicator of perturbation in recreational lakes

**Daniel Lambert, Antonella Cattaneo, and Richard Carignan**

**Abstract:** We looked for empirical relationships between periphyton biomass and recreational development in the Laurentian lakes of Quebec (Canada). We compared the response of periphyton (as chlorophyll *a*) on rocks and sediments with that of phytoplankton. Epilithon and epipelon biomass increased significantly with lake recreational development (as percentage of cleared land within a 50 m riparian strip) but was not related with open-water phosphorus concentration. In contrast, phytoplankton was related to open-water phosphorus but did not increase along the gradient of lake development. Periphyton stoichiometric composition also changed with increasing lake development. High C:P and C:N ratios were found in pristine lakes, whereas lower periphyton molar ratios, which approached the optimal stoichiometric composition for benthic microalgae, were observed in the most developed lakes. Our findings suggest that periphyton, positioned near the land–water interface, has access to land-derived nutrients before they are diluted in the open water. Therefore, periphyton on all substrata is the first community to respond to increased inputs resulting from lake recreational development. The measurement of littoral algal biomass and chemical composition may represent a better tool for early detection of lake perturbation than classic methods based on pelagic characteristics.

**Résumé :** Nous avons recherché des relations empiriques entre la biomasse du périphyton et l'importance de la villégiature dans des lacs des Laurentides au Québec (Canada). Nous comparons la réaction du périphyton (chlorophylle *a*) sur les pierres et les sédiments à celle du phytoplancton. La biomasse de l'épilithon et celle de l'épipélon augmentent significativement en fonction de l'importance de la villégiature (le pourcentage de terres défrichées dans une bande de rivage de 50 m), mais non en fonction de la concentration de phosphore en eau libre. En revanche, le phytoplancton est en corrélation avec le phosphore en eau libre, mais il n'augmente pas en fonction du gradient de l'importance de la villégiature. La composition stoichiométrique du périphyton change aussi en fonction de l'importance de la villégiature. On observe des rapports élevés de C:P et C:N dans les lacs encore sauvages, alors que les rapports molaires du périphyton sont plus bas dans la plupart des lacs à villégiature où ils s'approchent de la composition stoichiométrique optimale pour les microalgues benthiques. Nos observations indiquent que le périphyton, qui se développe près de l'interface terre–eau, a accès aux nutriments qui proviennent du sol avant que ceux-ci ne soient dilués dans la masse d'eau libre. Ainsi, le périphyton sur tous les substrats est la première communauté à réagir aux apports accrus consécutifs au développement de la villégiature. La détermination de la biomasse et de la composition chimique des algues littorales peut donc s'avérer être un outil plus efficace pour déceler tôt la perturbation des lacs que les méthodes classiques basées sur les caractéristiques pélagiques.

[Traduit par la Rédaction]

## Introduction

Increasing population, the desire to escape from urban life to nature, and the country retirement of baby boomers are all factors leading to further recreational development in previously pristine lakes. Construction of new dwellings and clearing of riparian shores alter the nutrient input to these lakes (Moore et al. 2003). Early detection of change is particularly important in these clean lakes to prevent them reaching a eutrophic state. There are some suggestions that increasing nutrient loading to an oligotrophic lake may affect periphyton biomass and production before that of phytoplankton (Sand-Jensen and Borum 1991; Planas et al. 2000). However, lake management models are mostly based on open-water characteristics (e. g. Dillon and Rigler 1974). The use of periphyton for monitoring eutrophication is still limited, probably because attempts to relate periphyton biomass to water nutrients have largely failed (Cattaneo 1987; Hansson 1992). This failure has been partly ascribed, at least for the epipelon that is in close contact with interstitial waters, to the fact that open-water nutrients do not fully represent those available to littoral algae.

Here, we look for empirical relationships between periphyton biomass and recreational development in the Laurentian lakes of Quebec (Canada). Since 1970, dwelling density in this region has more than doubled, and the proportion of

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cottages used yearlong has substantially increased (Laurin 2000). This development led to increased clearing of forests for buildings, lawns, parking lots, and roads, mainly concentrated along the lakeshore. We sampled algae on rocks (epilithon) and sediments (epipelon), which are the most common natural substrata in these lakes. The response of these two communities to shore development may be different because epilithon does not receive nutrients from its substratum, while epipelon can draw nutrients from sediments (Carlton and Wetzel 1988; Hansson 1989). We compared the response (as chlorophyll *a*, Chl *a*) of periphyton to that of phytoplankton, the most commonly used target variable in eutrophication studies. In addition, we measured C, N, and P proportions in periphyton because molar ratios may be indicative of nutrient availability (Stevenson 1996) and, unlike biomass, are not expected to be affected by losses due to grazing and sloughing. Furthermore, the value of periphyton as a food source for grazers, and thus its importance in the trophic chain, depends on its elemental ratio (Frost et al. 2002*b*).

## Materials and methods

### Study site

We studied 18 lakes in the Laurentian region of Quebec situated north of Montréal on the Canadian Shield within a 65 km radius from the Station de Biologie des Laurentides (45°59′N, 73°60′W). This region is experiencing increasing recreational development whereas agriculture and industrial activity are negligible. We chose the lakes to represent the typical span in size, depth, and watershed development going from pristine (no dwellings) to moderately inhabited (maximum 340 dwellings·km$^{-2}$) (Table 1). Most dwellings in this region are not serviced by municipal sewers but are instead connected to individual septic systems.

### Sampling

In the summer of 2003, we sampled 13 lakes on three occasions (May, June, and August). In 2004, we revisited these 13 lakes on four occasions (May, June, July, and August), adding five new lakes to increase the range of physical and chemical variables. We collected periphyton on rocks (epilithon) and sediments (epipelon) in both years. On each lake, we sampled eight sites distributed regularly around the lake perimeter. A 60 mL cut-off syringe was used to collect a 4.9 cm$^2$ sediment core. The first superficial centimetre of the core was kept and frozen for Chl *a* analysis of the epipelon. On rocks, epilithon was collected with a brush–syringe sampling device (4.9 cm$^2$; Loeb 1981) and transferred into a plastic container. All samples were collected by divers at ~1 m depth where light was not limiting and where wave disturbance was reduced. Preliminary samplings had indicated that depth gradients in periphyton Chl *a* were not pronounced in these lakes (A. Cattaneo, unpublished data).

In the laboratory, epilithon samples were filtered on Gelman type A/E glass-fiber filters (1 µm pore size), which were kept frozen until analysis. Chl *a* concentrations were measured before and after acidification at 665 and 750 nm (Spectronic Genesys 5 spectrophotometer) after extracting filters in 95% ethanol for 24 h (Nusch 1980). Epipelon samples were freeze-dried before Chl *a* extraction with ethanol (Hansson 1988).

**Table 1.** The range (mean) in watershed and lake characteristics observed in the 18 lakes studied in the Laurentian region of Quebec.

| Parameter | Range (mean) |
|---|---|
| Area (km$^2$) | 0.07–2.80 (0.61) |
| Volume ($10^3$ m$^3$) | 296 – 37 276 (6817) |
| $Z$ (m) | 4.2–24.4 (9.0) |
| $Z_{max}$ (m) | 10–60 (22) |
| Drainage area (km$^2$) | 0.22–24.36 (6.77) |
| Dwellings·km$^{-2}$ within all drainage area | 0–340 (69) |
| Dwellings·km$^{-2}$ within a 50 m wide riparian strip | 0–686 (238) |
| Cleared land (% within all drainage area) | 0–53 (10) |
| Cleared land (% within a 50 m wide riparian strip) | 0–86 (30) |
| Catchment average slope (°) | 5.9–14.6 (9.1) |
| TP (µg·L$^{-1}$) | 3.8–12.9 (7.5) |
| TDP (µg·L$^{-1}$) | 1.4–4.3 (2.5) |
| TN (µg·L$^{-1}$) | 202.6–488.2 (335.4) |
| $NO_3$ (µg·L$^{-1}$) | 10.0–121.4 (54.4) |
| DOC (mg·L$^{-1}$) | 2.2–5.4 (3.3) |
| Secchi depth (m) | 2.5–9.0 (5.4) |

**Note:** Chemical variables are the mean values of four samplings in summer 2004. $Z$, depth; TP, total phosphorus; TDP, total dissolved phosphorus; DOC, dissolved organic carbon.

Samples for C, N, and P analyses were collected in June and August 2003 at four sites around each lake on rocks and sediments using the same methods described above. Epilithon was concentrated by centrifugation, frozen, and freeze-dried. The samples were then homogenized with mortar and pestle before C and N determination with a Fisons Elemental Analyser 1108 CHNS-O. Phosphorus content was determined after autoclaving an aliquot (~5 mg) of the homogenized sample suspended in 50 mL of water with 0.5 g of potassium persulfate for 45 min at 120 °C (Stainton et al. 1977). This technique gave similar results to the one using sequential heating and sulfuric acid (Hillebrand and Sommer 1997), but required less material.

Lake water samples were collected near the deepest point of each lake contemporaneously to the littoral sampling. Integrated samples over the entire euphotic zone (defined as 1.7 times the Secchi depth) were collected with a polyvinyl chloride (PVC) tube in duplicate (2003) and triplicate (2004) and kept refrigerated for 12–24 h until analysis. Unfiltered subsamples were used for total phosphorus (TP) and total nitrogen (TN) analyses. Water was filtered through 0.45 µm membrane filters (Life Sciences Super®-450) for total dissolved phosphorus (TDP), nitrate ($NO_3$), and dissolved organic carbon (DOC) analyses. Subsamples for Chl *a* measurements (Nusch 1980) were filtered through Gelman type A/E glass-fiber filters (1 µm pore size). TP and TDP samples were analysed as orthophosphate (Stainton et al. 1977) after persulfate digestion in an autoclave. TN and $NO_3$ were analysed with a LACHAT Continuous Flow QuikChem 8000 and DOC with a Shimadzu TOC-5000A analyser.

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Dwelling density and cleared land surface area were measured (MapInfo version 6.5, MapInfo, Troy, New York) on 1:10 000 or 1:30 000 orthorectified aerial photographs taken in 2002 and 2004. Cleared land represented areas with buildings, roads, parking lots, and lawns; in two instances, a golf course and ski trails were also included. Because watershed development in this region is usually concentrated around the lakeshore, we measured landscape characteristics not only in the entire drainage area but also in various riparian strips of increasing width (50, 100, 200, 500, 1000 m). Watershed (area and slope) and lake morphological characteristics (area, volume, and maximum depth) were measured (MapInfo) from numerical topographic and bathymetric maps.

### Statistical analyses

Periphyton and phytoplankton biomass and periphyton molar ratios were related with land use descriptors, open-water chemical concentrations, and lake and watershed morphological characteristics through correlation and regression analyses. Differences in periphyton biomass between sampling dates within a summer were tested by analysis of variance (ANOVA). Differences in average summer biomass between the two study years were tested by paired $t$ test ($n$ = 13). Normality test (Wilk–Shapiro) indicated that data did not require transformation. All statistical analyses were performed with Statistix (Analytical Software, Tallahassee, Florida).

## Results

### Environmental characteristics of the lakes

Only 3 of the 18 lakes may be considered slightly mesotrophic (Organization for Economic Cooperation and Development 1982), with mean summer TP exceeding 10 $\mu g \cdot L^{-1}$ (10.6, 12.2, and 12.9) and mean summer TN above 400 $\mu g \cdot L^{-1}$ (451, 467, and 488) (Table 1). Mean summer TP and TN varied respectively by 3.5- and 2.4-fold among lakes. The lake set comprised clear and coloured lakes, with mean summer DOC ranging from 2.2 to 5.7 $mg \cdot L^{-1}$. Overall weather conditions were similar for the 2 years of the study. Summer (April–August) 2003 was slightly warmer (13.2 °C) than summer 2004 (12.9 °C), but they were both under the seasonal average (13.5 °C). Total summer precipitation was higher in 2003 (412 mm) than in 2004 (381 mm), and both years were below the seasonal average (496 mm). Seasonal averages are based on data registered between 1970 and 1988 by Environment Canada at our nearby Saint-Hippolyte field station (7037310).

### Temporal patterns of periphyton biomass

Our sampling covered two consecutive years and different dates over the growing season to represent typical summer periphyton development in these lakes. When considering all the lakes, there were no significant seasonal pattern in the biomass of epilithon and epipelon either in 2003 (ANOVA, $p$ = 0.10 and $p$ = 0.98, respectively) or in 2004 (ANOVA, $p$ = 0.85 and $p$ = 0.40, respectively). To test whether watershed development level might affect the seasonal pattern, we grouped the lakes into three categories according to the amount of cleared land (as a percentage) within the first 50 m of riparian zone (low, <15%; medium, 15%–35%; high, >35%; Fig. 1). There were no significant seasonal patterns in any group for epilithon (ANOVA, all $p > 0.11$) and for epipelon (ANOVA, all $p > 0.31$). Because periphyton biomass was roughly constant throughout the summer, further analyses were limited to summer averages.

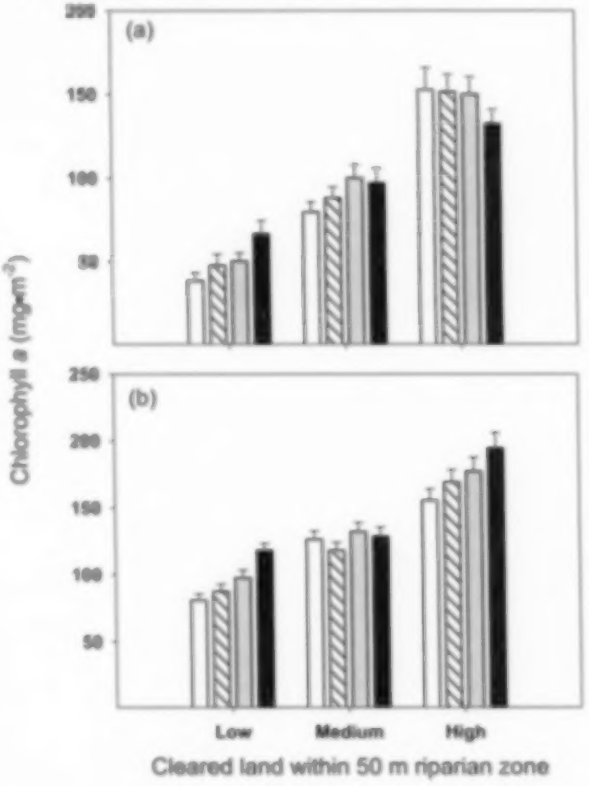


**Fig. 1.** Seasonal changes in epilithon (*a*) and epipelon (*b*) biomass (Chl *a*) observed in 2004 in lakes of the Laurentian region grouped according to the degree of clearing within a 50 m strip around the lakeshore (low, <15%; medium, 15%–35%; high, >35%). Bars represent the mean with standard error ($n$ = 6). Sampling dates are indicated by different shading patterns: May (open), June (hatched), July (gray), August (solid).

Periphyton summer biomass was slightly higher in 2004 than in 2003 (24% for epilithon and 11% for epipelon). This difference was significant for both epilithon and epipelon (paired $t$ test, $n$ = 13, $p$ = 0.02 and $p$ = 0.03, respectively). We kept the data for the 2 years separate because they were based on a different number of lakes (13 in 2003 and 18 in 2004).

### Periphyton and phytoplankton relationships with watershed development and open-water chemistry

Periphyton biomass on rock and on sediment was significantly correlated with two descriptors of watershed development: dwelling density and percentage of cleared land (Fig. 2). Correlation coefficients were higher when these variables were measured in narrow riparian strips (50 m for percentage of cleared land and 100 m for dwelling density), rather than considering the entire watershed. Overall, in both

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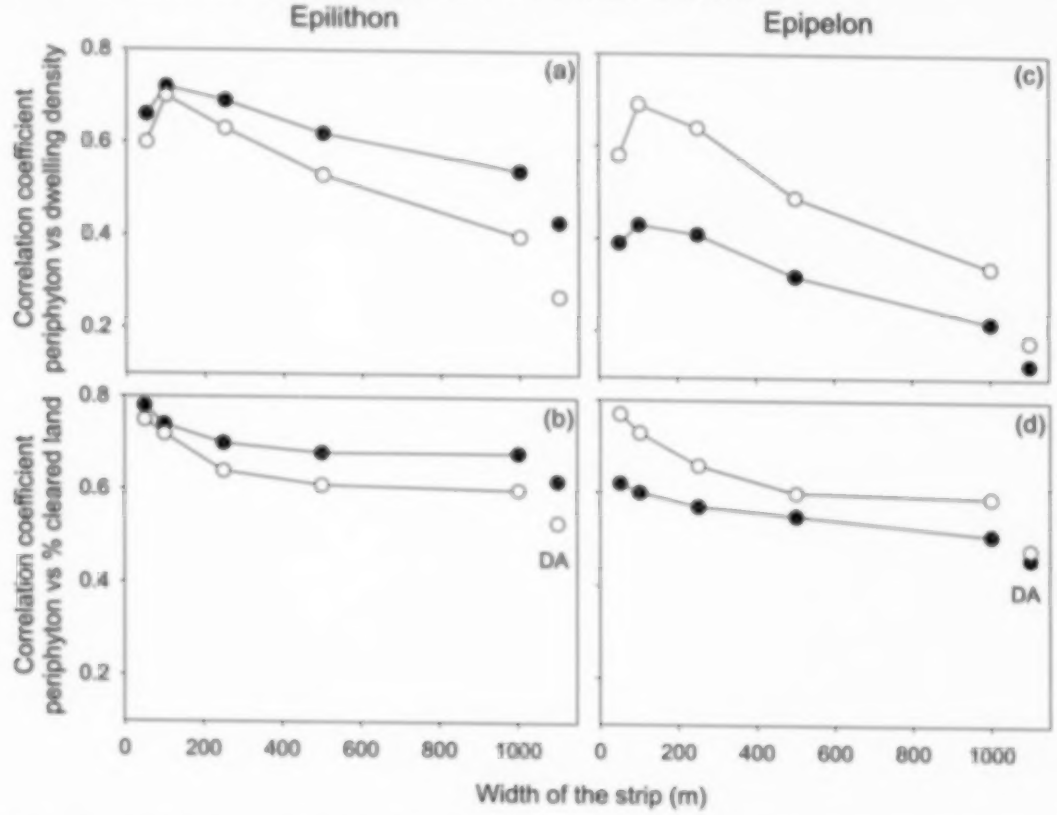
**Fig. 2.** Correlation coefficients between epilithon (*a*, *b*) and epipelon (*c*, *d*) biomass (Chl *a*) and two descriptors of watershed development (dwelling density and percentage of cleared land) measured within strips of increasing width and within the entire drainage area (DA) in 2003 (solid symbols) and in 2004 (open symbols). $n = 13$ in 2003; $n = 18$ in 2004.




years, the best models of periphyton biomass were found when considering the percentage of cleared land in a 50 m riparian strip (Fig. 2). Epilithon (as Chl *a*) changed more than epipelon along the development gradient. In the less perturbed lakes, biomass on sediments was more than twice as high as that on rocks, whereas in the more developed lakes it was similar on the two substrata (Figs. 3*a*, 3*d*).

Epilithon biomass was not significantly related to any of the watershed (drainage area and slope) and lake morphometric variables (surface area, volume, mean and maximum depth). Epipelon biomass had a weak but significant correlation with the ratio of watershed area to lake area ($r = 0.39$, $p = 0.04$). Epilithon and epipelon biomass were not correlated with variables measured in the open water (TP, TDP, DOC, and Secchi depth) except with TN (Figs. 3*c*, 3*f*). Epipelon was also significantly correlated with $NO_3^-$ concentration ($r = 0.37$, $p = 0.04$).

In contrast with periphyton, phytoplankton Chl *a* was not related to descriptors of watershed development (Fig. 4*a*). Instead, phytoplankton was positively related with TP (Fig. 4*b*), but not with TN (Fig. 4*c*).

### Periphyton stoichiometric composition

Epilithon and epipelon molar ratios (C:P, C:N, N:P) significantly decreased along the gradient of watershed development. As for periphyton biomass, the relationships between molar ratios and percentage of cleared land improved when considering narrow riparian strips. The best relationships were observed when the 50 m strips were considered (Fig. 5). Molar ratios decreased significantly with increasing periphyton biomass with the sole exception of epipelon N:P (Table 2).

## Discussion

Our results confirmed earlier observations (Cattaneo 1987; Hansson 1992) that relationships between periphyton biomass and water phosphorus are weak. Light interactions over a trophic gradient, observed in other studies (DeNicola et al. 2003), could be ruled out here because these lakes were all transparent (Secchi depth always >2.5 m), and samples were collected at 1 m. Periphyton P relationships could be weak because the concentrations measured in the open water did not coincide with those available to the attached algae. Instead, epilithon and epipelon were both significantly correlated with lakeshore development, expressed either as dwelling density or forest clearing. This perturbation may change the physical environment of periphyton, increasing light availability and temperature. However, increased nutrient inputs are the mechanism most likely to be related to

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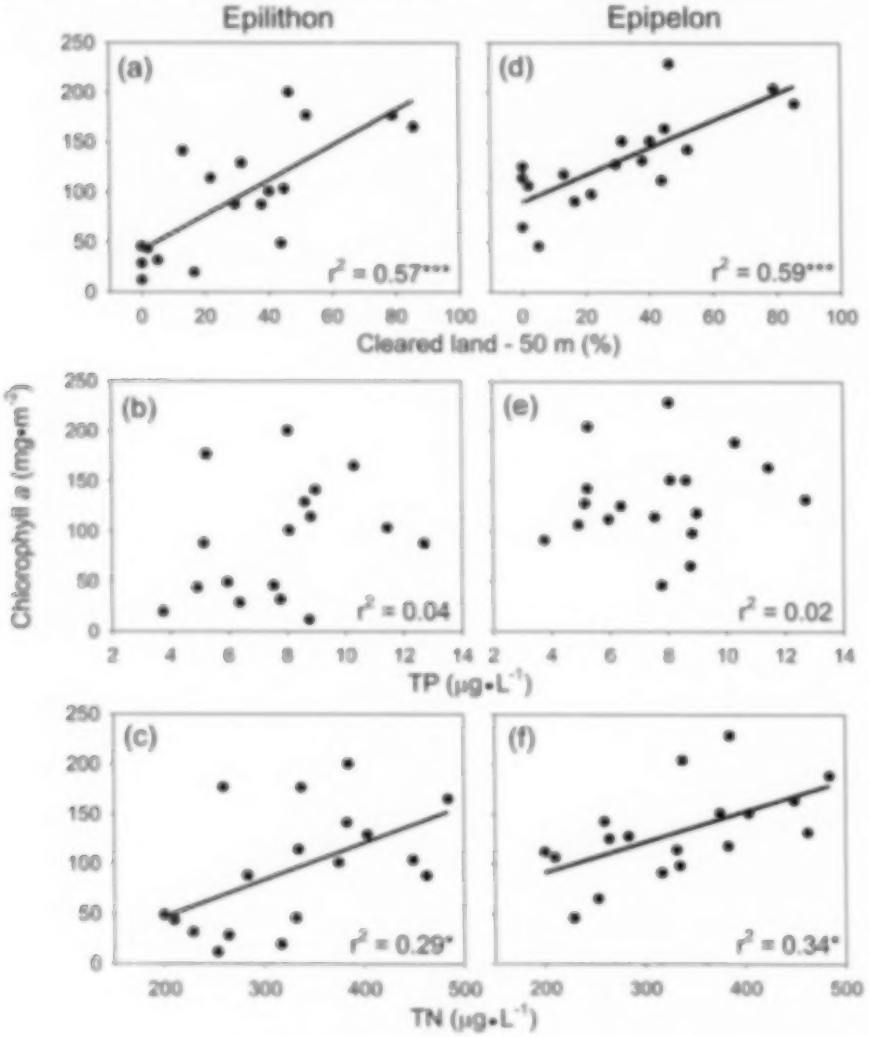
**Fig. 3.** Relationships of epilithon and epipelon biomass (Chl *a*) with percentage of cleared land within a 50 m wide strip around the lake (CL; *a*, *d*), water total phosphorus (TP; *b*, *e*), and total nitrogen (TN; *c*, *f*). Values of $r^2$ are presented for all relationships where $n = 18$ (*, $p < 0.05$; ***, $p < 0.001$). Regression lines are shown only for the significant relationships: (*a*) Chl $a_{epilithon} = 42.5 + 1.74 \cdot CL$; (*c*) Chl $a_{epilithon} = 0.37 \cdot TN - 27.3$; (*d*) Chl $a_{epipelon} = 90.5 + 1.35 \cdot CL$; (*f*) Chl $a_{epipelon} = 0.31 \cdot TN - 29.5$.




periphyton growth. Phosphorus export from watersheds of this region was strongly correlated to percentage of cleared land (Carignan et al. 2006). Periphyton, positioned near the land–water interface, may have access to land-derived nutrients before they are diluted in the open water. This mechanism has been demonstrated for epipelon growing on the sediments and relying on interstitial water (Carlton and Wetzel 1988; Hansson 1988). Being attached to an inert substratum, epilithon is supposed to respond to open-water nutrients like phytoplankton (Vadeboncoeur et al. 2006). Nevertheless, littoral epilithon should be exposed to relatively high nutrient concentrations compared with those observed in open waters wherever substantial nutrient loading occurs from the shoreline. As expected, phytoplankton chlorophyll was significantly related with open-water TP but changed little (maximum–minimum: 3-fold) and not proportionally along the development gradient. The stronger response of epilithon (maximum–minimum: 13-fold) compared with phytoplankton could be explained by the fact that it is possible for attached algae to accumulate on their substratum over long periods of time, whereas such accumulation of suspended algae is prevented by sedimentation and flushing. Furthermore, close algal–microbial proximity is supposed to make nutrient retention and recycling more efficient in periphyton than in phytoplankton (Wetzel 1996).

It has been repeatedly observed in oligotrophic lakes that epipelon reaches a higher biomass than epilithon (Vadeboncoeur et al. 2006). In the Laurentian lakes, we observed that the difference in biomass between substrata decreased with shore development. As a result, epilithon varied much more

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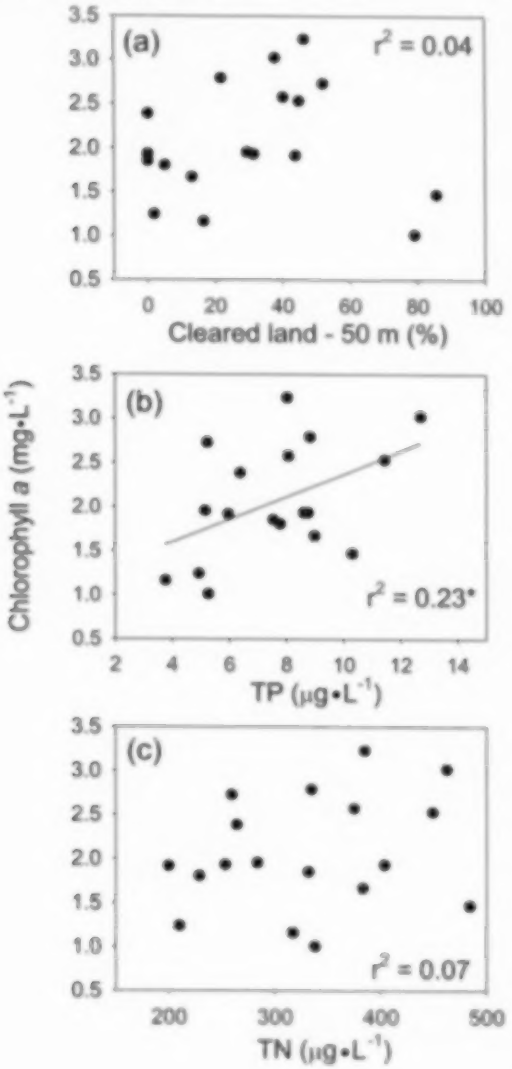
**Fig. 4.** Relationships of phytoplankton biomass (Chl *a*) with percentage of cleared land within a 50 m wide strip around the lake (*a*), water total phosphorus (TP; *b*), and total nitrogen (TN; *c*). Values of $r^2$ are presented for all relationships where $n = 18$ (*, $p < 0.05$). Regression line is shown only for the significant relationship (*b*): Chl $a_{phytoplankton} = 1.09 + 0.13$·TP.




than epipelon along the gradient. Epilithon should be disadvantaged in the most oligotrophic lakes, because unlike epipelon, which gains nutrients from porous sediments, it cannot draw nutrients from its rock substratum. Once inputs from shore development enter the lakes, both epilithon and epipelon can increase in biomass. However, changes in periphyton biomass along the development gradient would be especially noticeable on rocks, varying from extremely low values to levels similar to those on sediments.

Variables describing land development (dwelling density and forest clearing) were more closely related to periphyton biomass when expressed per unit area of narrow (50–150 m) buffer strips laid around the lakes. This reflects the fact that residential development of these lakes typically occurs near the shore, leaving the rest of the watershed mostly untouched. Nutrient concentrations in the open water were related to lakeshore development when expressed per unit lake volume (Carignan et al. 2006). The impact of lakeshore development on periphyton was instead independent of lake volume, again suggesting that the effect of nutrient inputs was local at the edge of the lake rather than diluted according to water volume.

The changes in C:N:P ratios in periphyton along the gradient of lakeshore residential development were further evidence of periphyton enrichment. Molar ratios decreased to approach the optimal value for benthic microalgae (C:N:P = 119:17:1; Hillebrand and Sommer 1999) with increasing forest clearing near the shore. The transition from naturally vegetated shores to developed land may increase the export of dissolved P (Frink 1991) that is readily available for uptake by littoral algae. High N:P and C:P ratios in the epilithon of the most pristine lakes suggest severe P limitation. The high C:P ratios we observed were in a similar range to those measured in other oligotrophic lakes of the Canadian Shield (Frost et al. 2002*a*). These high values probably reflect the presence of a large amount of detritus originating from riparian soil and vegetation, which is high in C in the Canadian Shield (Hecky et al. 1993). In fact, there may be a large proportion of detritus in periphyton from oligotrophic lakes (Frost et al. 2005). Phosphorus enrichment leads to increased periphyton biomass and therefore to a higher proportion of algal material in the total particulate organic matter. Periphyton biomass was significantly higher when nutrients molar ratios were low, implying that the most developed lakes were receiving increased nutrients, especially P, which supported higher periphyton biomass.

Epipelon was also nutrient-limited. Although C:P ratios were lower in epipelon than in epilithon, C:N and N:P ratios indicated a more severe N limitation on sediments than on rocks. The elevated C:N ratios of epipelon in the undeveloped, pristine lakes were probably related to a high level of terrestrial plant detritus that decomposes slowly and has C:N ratios over 30 (Gosz et al. 1973). With increasing riparian clearing, plant detritus in lakes decreases (Christensen et al. 1996). This occurrence, coupled with higher nutrient loading that reduces nutrient limitation, led to low molar ratios and high epipelon biomass in the developed lakes.

In conclusion, nutrient concentrations and phytoplankton Chl *a* remained low throughout a large range of lakeshore development. Values slightly exceeded those typical of oligotrophic lakes (Organization for Economic Cooperation and Development 1982) in only three instances. In contrast, periphyton Chl *a* was already beyond the value of 100 mg·m$^{-2}$, generally considered as the beginning of nuisance conditions (Dodds et al. 1997), in more than half of the lakes (9 for epilithon and 12 for epipelon). Whole-lake (Vadeboncoeur et al. 2001) and mesocosm (Blumenshine et al. 1997) experimental fertilization have shown a strong response of algae on hard substrata but not of those on sediments. To our knowledge, this study provides the first demonstration in unmanipulated lakes of the same region that periphyton on all substrata respond more than phytoplankton to increasing lakeshore development. Nutrient enrich-

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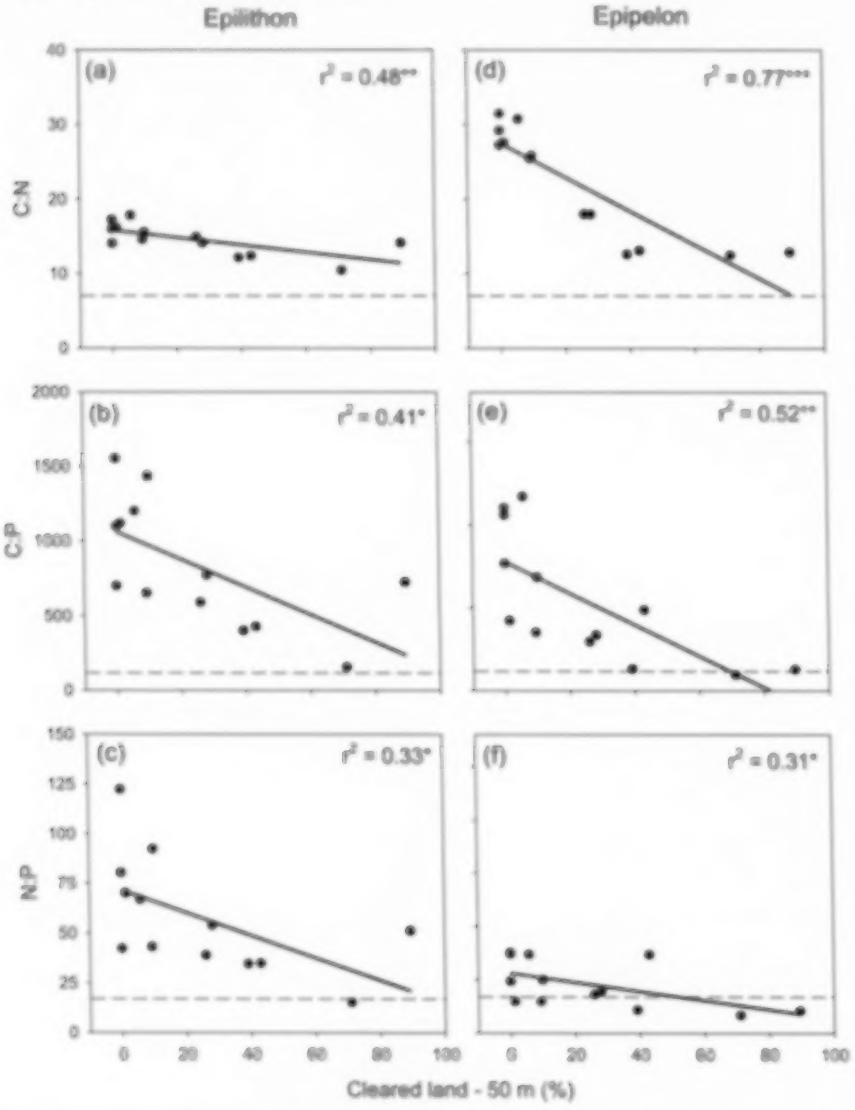
**Fig. 5.** Relationships of epilithon (*a*, *b*, *c*) and epipelon (*d*, *e*, *f*) nutrient molar ratios and the percentage of cleared land inside a 50 m wide strip around the lake. Regression lines and $r^2$ are presented for all relationships where $n = 13$ (*, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$). Lakes over broken lines are considered N-limited (*a*, *d*) or P-limited (*b*, *c*, *e*, *f*), according to optimal stoichiometric ratios (C:N:P = 119:17:1) proposed by Hillebrand and Sommer (1999).




ment following fires or harvesting in the watershed enhanced benthic production more than pelagic production (Planas et al. 2000). These findings have important implications for lake management.

Considerable efforts by state agencies and resident associations are directed to measuring open-water characteristics (Secchi depth, phytoplankton Chl *a*, and TP) to set management guidelines and to monitor the evolution of lake trophic state. This strategy may provide misleading results for lakes experiencing recent recreational development. In the Laurentian lakes, the development of littoral algae responded more to lakeshore perturbation than phytoplankton did. Warning signs may appear in the open water too late to control the

**Table 2.** Correlation coefficients ($r$) between periphyton biomass (as Chl *a*) and nutrient molar ratios where $n = 13$.

| Biomass (Chl *a*) | Molar ratio | $r$ |
|---|---|---|
| Epilithon | C:P | −0.84*** |
| | N:P | −0.78** |
| | C:N | −0.81*** |
| Epipelon | C:P | −0.57* |
| | N:P | −0.41 |
| | C:N | −0.75** |

Note: *, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$.

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undesirable changes in the aesthetics and biodiversity of a lake that accompany eutrophication. Periphyton is the first to respond to the nutrients mobilized by watershed development, and thus the measurement of its biomass and chemical composition may represent a simple alternative tool to classic methods for early detection of lake perturbation.

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# Water velocity influences prey detection and capture by drift-feeding juvenile coho salmon (*Oncorhynchus kisutch*) and steelhead (*Oncorhynchus mykiss irideus*)

**John J. Piccolo, Nicholas F. Hughes, and Mason D. Bryant**

**Abstract:** We examined the effects of water velocity on prey detection and capture by drift-feeding juvenile coho salmon (*Oncorhynchus kisutch*) and steelhead (sea-run rainbow trout, *Oncorhynchus mykiss irideus*) in laboratory experiments. We used repeated-measures analysis of variance to test the effects of velocity, species, and the velocity × species interaction on prey capture probability, prey detection distance, and swimming speeds during prey capture. We used 3D video analysis to assess the spatial and temporal characteristics of prey detection and capture. Coho and steelhead showed significant, velocity-dependent decreases in capture probability (~65% to 10%, with an increase of velocity from 0.29 to 0.61 $m \cdot s^{-1}$) and prey detection distance, with no effect of species and no velocity × species interaction. Neither velocity nor species affected prey interception speed; fish intercepted prey at their predicted maximum sustainable swimming speed ($V_{max}$) at all velocities. Speed of return to the focal point increased significantly with increasing velocity, with no effect of species. At faster velocities, return speeds were faster than $V_{max}$, indicating potential increases in energetic cost because of anaerobic swimming. The 3D analysis suggests that the reduction in capture probability was due to both reduced prey detection distance and a uniform decline in detection probability within the prey capture area.

**Résumé :** Nous examinons lors d'expériences en laboratoire l'effet de la vitesse du courant sur la détection et la capture des proies chez de jeunes saumons coho (*Oncorhynchus kisutch*) et truites arc-en-ciel anadromes (*Oncorhynchus mykiss irideus*) qui se nourrissent dans la dérive. Une analyse de variance à mesures répétées a permis de tester les effets de la vitesse du courant, de l'espèce et de l'interaction vitesse × espèce sur la probabilité de capture des proies, la distance de détection des proies et la vitesse de nage durant la capture des proies. Une analyse vidéo 3D a servi à déterminer les caractéristiques spatiales et temporelles de la détection et de la capture des proies. Les saumons et les truites connaissent des diminutions significatives des probabilités de capture (~65 % à 10 % lors d'une augmentation de vitesse de 0,29 à 0,61 $m \cdot s^{-1}$) et de la distance de détection des proies en fonction de la vitesse de courant; l'espèce et l'interaction vitesse × espèce restent sans effet. Ni la vitesse du courant, ni l'espèce n'affectent la vitesse d'interception des proies; les poissons interceptent les proies à leur vitesse maximale prédite de nage soutenue ($V_{max}$) à toutes les vitesses du courant. La vitesse de retour au point focal augmente significativement en fonction de la vitesse du courant, mais sans effet de l'espèce. Aux vitesses du courant les plus grandes, la vitesse de retour dépasse $V_{max}$, ce qui indique un accroissement potentiel du coût énergétique à cause de la nage anaérobie. L'analyse 3D laisse croire que la réduction de la probabilité de capture peut être due autant à la diminution de la distance de détection de la proie qu'à un déclin uniforme de la probabilité de détection dans la zone de capture des proies.

[Traduit par la Rédaction]

## Introduction

Stream salmonids often drift-feed, maintaining a position in the stream channel and capturing invertebrate prey as it is delivered by the current (Bachman 1984; Fausch 1984; Hughes and Dill 1990). For drift feeders, selecting a position in faster water is assumed to be a trade-off between the benefit of encountering more prey (i.e., encounter rate) and the energetic cost of foraging in faster water (Fausch 1984; Hill and Grossman 1993). Ecologists have incorporated drift

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feeding into energetics-based models that predict stream salmonid distribution (Hughes and Dill 1990; Hughes 1992; Guensch et al. 2001), energy intake (Hill and Grossman 1993; Hughes et al. 2003), and growth (Hughes 1998; Hayes et al. 2000; Nislow et al. 2000). Water velocity plays an important role in these models because it determines the prey encounter rate, the probability that a fish will capture a prey (i.e., capture probability), and the swimming costs for a fish at a given stream position (Fausch 1984; Hill and Grossman 1993; Hughes et al. 2003). To date, researchers have found that drift-foraging models are more sensitive to changes in benefits (e.g., prey encounter rate) than they are to changes in costs (Hughes and Dill 1990; Hill and Grossman 1993, but see Hughes et al. 2003 for a discussion of prey capture costs). This underscores the importance of identifying how water velocity affects the fish's ability to detect (i.e., observe) and capture prey. Hughes et al. (2003) noted that developing models to more accurately predict energy intake rates of drift feeders will require a better understanding of how habitat factors such as water velocity influence a prey detection and capture probability.

Despite the importance of water velocity in drift-foraging models, few studies have addressed how velocity influences capture probability in drift-feeding salmonids. Increasing velocity may reduce the distance at which prey are detected or captured (i.e., detection and capture distance) (Godin and Rangeley 1989; Hill and Grossman 1993; O'Brien and Showalter 1993). O'Brien et al. (2001) found that increasing water velocity decreased capture probability and capture distance for Arctic grayling (*Thymallus arcticus*), but they did not find an expected increase in foraging rate (number of prey captured per unit time). They suggested this may be due to a trade-off between increasing encounter rate and decreased prey detection ability as water velocity increases. They also found that the amount of time searching for prey (search time) and the time it took to intercept prey (interception time) were not affected by water velocity. This is important because drift-foraging models rely on estimates of these times (Hayes et al. 2000; Guensch et al. 2001; Hughes et al. 2003), but to date little is known about how water velocity influences these times.

Although drift-foraging models have been used to predict habitat selection for two or more sympatric species (Hill and Grossman 1993; Braaten et al. 1997; Guensch et al. 2001), there have been no comparisons of the effects of water velocity on two sympatric drift feeders. This represents a gap in our understanding of habitat selection, because velocity-based habitat segregation has been documented for a number of sympatric pairs of salmonids (Hartman 1965; Everest and Chapman 1972; Bremset and Berg 1999). If fish segregate habitat based on their potential to maximize net energy intake (energetic gains minus energetic costs) at their respective positions (e.g., Fausch 1984; Hill and Grossman 1993), it ought to be possible to identify the mechanism that allows them to do so at different velocities. Werner and Hall (1979), for example, showed that differences in body morphology among three species of sunfish facilitated habitat segregation based on foraging efficiency. Differences in body morphology have been suggested as one explanation for habitat segregation in stream salmonids (Bisson et al. 1988), but no experimental tests have confirmed this.

Juvenile coho salmon (*Oncorhynchus kisutch*) and steelhead (sea-run rainbow trout, *Oncorhynchus mykiss irideus*) occur sympatrically in freshwater streams (Groot and Margolis 1991; Behnke 1992; Nakano and Kaeriyama 1995), where they often drift-feed (Everest and Chapman 1972; Nielsen 1992). Although they are found within the same stream reaches, they have been documented to segregate microhabitat, with coho using pools and steelhead using riffles (Hartman 1965; Bisson et al. 1988; Bugert and Bjornn 1991). Bisson et al. (1988) proposed that coho may be better adapted to forage in pools because they have a laterally compressed body form with long median fins, which facilitates rapid turning and acceleration. Steelhead may be better adapted to foraging in riffles because they have a more cylindrical body form with shorter median fins, which minimizes drag during foraging maneuvers.

Our objective was to assess the influence of water velocity on prey detection and capture by juvenile coho and steelhead. We used three-dimensional (3D) video analysis of stream tank foraging experiments to test these hypotheses: (*i*) capture probability declines with increasing water velocity, and (*ii*) there are species-specific differences in capture probability, prey detection distance, prey interception speed, and speed of return to the focal point that might facilitate foraging in their respective preferred habitats.

## Materials and methods

### Stream tank

We constructed a variable-depth and -velocity stream tank to allow precise adjustment of water velocity (Fig. 1). The experimental arena measured 1.5 m long × 1 m wide × 0.3 m deep, enclosed at each end with mesh screens. A Plexiglas window on one side allowed us to videotape the experiments. The remainder of the arena was painted a light blue-green color. A 0.10 m × 0.10 m grid of dots were drawn on the viewing window and the back wall to allow 3D analysis of video data (see below). The substrate was ~0.01 m diameter gravel. One flat, ~0.1 m diameter rock was placed near the center of the tank to serve as a focal point. Prey were delivered through the upstream screen via any one of 20 plastic feeder tubes (6.25 mm diameter) arranged in two layers of 10 each, equally spaced, at layers 0.1 and 0.2 m deep. Uneaten prey were filtered out by a 0.625 mm mesh stainless steel screen so they could not recirculate.

### Experimental protocol

Nineteen wild fish of each species were collected from the West Fork of the Situk River near Yakutat, Alaska, in June 2001. Fish measured 70–80 mm fork length, which are presumed to be age 1+ based on length–frequency data (Lohr and Bryant 1999). All fish were collected from the same stream reach. Fish were shipped via air to Juneau, Alaska, and held in flow-through circular tanks. They were fed maintenance rations of frozen brine shrimp.

We conducted our experiments in a covered outdoor lab facility at the NOAA National Marine Fisheries Service Auke Bay Laboratory (Juneau, Alaska) in September–October 2001. Fresh water was supplied by a subsurface line from Auke Lake (mean water temperature was 10.46 °C (standard

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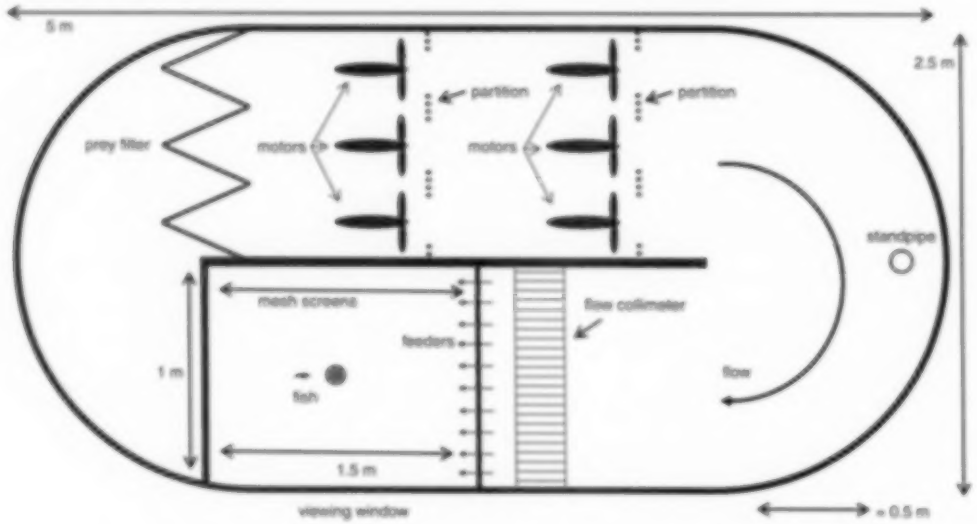
**Fig. 1.** Top-view diagram of the stream tank, drawn to approximate scale. Water velocity was provided by six Minn Kota EM44 electric trolling motors powered by 120 V AC to 12 V DC transformers. The motors raised the water pressure head on the downstream side of the partitions, pushing water through the flow collimeter (0.04 m diameter PVC pipe), providing relatively uniform velocity across the tank. Filtered water was added continuously to maintain water quality, and it drained through the standpipe, maintaining a depth of 0.30 m. Overhead light was provided by a 150 W full spectrum bulb, shaded to reduce glare. Light intensity was 500 lux at the water surface above the focal point.




deviation, SD = 0.84); mean dissolved oxygen was 7.78 mg·L$^{-1}$ (SD = 0.66); mean pH was 7.9 (SD = 0.21); mean turbidity was 0.36 nephelometric turbidity units (NTU; SD = 0.16). Photoperiod was maintained at 18 h day and 6 h night.

We selected five water velocity treatments, ranging from the minimum at which fish would hold station and drift-feed to near the maximum published value for 75 mm juvenile coho and steelhead (Everest and Chapman 1972; Beecher et al. 1993). Treatments were 0.29, 0.39, 0.48, 0.54, and 0.61 m·s$^{-1}$ mean water column velocity (measured at a point 0.20 m upstream from the focal point). At each treatment level, we made a detailed map of water velocity in the experimental arena by measuring velocity in 0.10 m × 0.10 m grids at three cross-sections, used for calculations of prey and fish speed (see Data analysis section below).

We randomly selected five fish of each species, ranging from 75 to 80 mm fork length, and paired by size between species. Experimental fish were held individually in 1 m × 0.3 m × 0.3 m flow-through raceways during the experimental period. Each fish was tested individually at each velocity, assigned in a random order with 2 days rest between treatments. Two species pairs of fish were tested each day, and the entire series of feeding trials was completed in as few days as possible to minimize any effects of time or growth (fish grew an average of 3.4 mm during experimental period). Fish were not fed for 24 h prior to a feeding trial to ensure they would be motivated to feed.

Before we began the entire series of experiments, each fish received a 15 min "warm-up" feeding trial to acclimate them to the experimental arena. Fish acclimated well to the experimental protocol, usually selecting a position behind the focal point rock and feeding within 1 min of being introduced to the tank. For each feeding trial, a fish was netted from its individual raceway and quickly released into the experimental arena at the slowest velocity. Velocity was stepped up gradually to the treatment level. A fish was observed to feed on at least one prey before the velocity was increased to the next level. When the test velocity was reached and the fish was observed to be actively feeding, the trial began. A feeding trial consisted of 100 individual prey being fed to a fish over a 25 min period (4 prey·min$^{-1}$). Prey were adult brine shrimp cut to 2 mm length to ensure that the fish's reaction distance to the prey (i.e., the furthest distance at which they react to and presumably detect prey) would be less than half of the tank width (Dunbrack and Dill 1984). Prey were randomly assigned to one of the 20 feeder locations and were fed at random times within each 15 s interval. At the conclusion of the experiment, fish were fed extra prey to be sure that they had not become satiated, and they were always observed to eat more prey.

We recorded our feeding trials on miniDV cassettes using two Sony GVD900 tape recorders and two Sony EVI 334 video cameras. Cameras were positioned at ~90° from each other relative to the fish focal point to facilitate 3D analysis.

## Data analysis

During the course of a 25 min experiment, each fish made a number of prey capture maneuvers. A maneuver consisted of a fish (*i*) detecting a prey, (*ii*) leaving the focal point and swimming to intercept the prey, and (*iii*) swimming to return to the focal point. All prey capture maneuvers for each fish were digitized using custom-designed computer software (Hughes and Kelly 1996). This allowed us to count the number of prey captured to calculate prey capture probability (the number of prey captured divided by 100, the total num-

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**Table 1.** Results of repeated measures analysis of variance (ANOVA) for the effects of water velocity, species, and the velocity × species interaction on prey capture characteristics of juvenile coho salmon (*Oncorhynchus kisutch*) and steelhead (sea-run rainbow trout, *Oncorhynchus mykiss irideus*) ($N$ = 5 of each species).

| Dependent variable | Source of variation | df | $F$ | $p$ |
|---|---|---|---|---|
| Prey capture probability | Water velocity | 4 | 117.71 | <0.0001 |
| | Species | 1 | 0.10 | 0.76 |
| | Velocity × species interaction | 4 | 1.23 | 0.32 |
| Prey detection distance | Water velocity | 4 | 17.60 | <0.0001 |
| | Species | 1 | 2.33 | 0.17 |
| | Velocity × species interaction | 4 | 2.24 | 0.09 |
| Interception speed | Water velocity | 4 | 1.31 | 0.29 |
| | Species | 1 | 1.46 | 0.26 |
| | Velocity × species interaction | 4 | 0.27 | 0.89 |
| Return speed | Water velocity | 4 | 247.05 | <0.0001 |
| | Species | 1 | 0.56 | 0.48 |
| | Velocity × species interaction | 4 | 0.39 | 0.82 |

ber of prey). It also provided the videotape timecode and the 3D coordinates ($x$ = upstream–downstream, $y$ = across-stream, and $z$ = vertical) for the nose and tail of the fish at the start, capture, and return point of each maneuver. To obtain the $x,y,z$ coordinates and times for each prey capture maneuver, we followed the following procedure: (*i*) Identify a prey capture maneuver on the tape and obtain the $x,y,z$ coordinates and time for the focal point location. (*ii*) Forward the tape to obtain the $x,y,z$ coordinates and time of the capture location when the fish closed its mouth on the prey. (*iii*) Define the difference of these times as the prey interception time. (*iv*) Estimate interception distance by assuming that the fish initiated a maneuver as soon as it detected a prey and that it swam in straight line to capture it. Once the fish leaves its focal point and enters the water column, it is displaced downstream at the same rate as is the prey; therefore, interception distance = detection distance. (*v*) Estimate the $x,y,z$ coordinates of the detection location by back-calculating the distance the prey had traveled along the $x$ axis from the capture location during the interception time and assuming the $y$ and $z$ positions did not change. (*vi*) Calculate the detection distance as the distance between the focal point coordinates (i.e., $x_1$, $y_1$, $z_1$) and the detection coordinates (i.e., $x_2$, $y_2$, $z_2$) using Pythagoras' theorem as follows:

$$\text{Distance} = \sqrt{(x_2 - x_1)^2 + (y_2 - y_1)^2 + (z_2 - z_1)^2}$$

(*vii*) Define return time as the time taken from interception until the fish returned to the focal point. (*viii*) Estimate the return distance by adding the amount of downstream ($x$ axis) displacement the fish experienced during the return time to the focal point location and calculating the distance between the capture location coordinates and this upstream point using Pythagoras' theorem. (*ix*) Calculate interception and return speeds by dividing distances by times. Front-, side-, and top-view figures of prey detection and capture locations were created by plotting the appropriate coordinates (front, $y,z$; side, $x,z$; top, $x,y$) after normalizing all focal point locations to the median and pooling by species ($N$ = 5).

We tested for the effects of water velocity, fish species, and the velocity × species interaction on (*i*) prey capture probability, (*ii*) mean prey interception distance, (*iii*) mean prey interception swimming speed, and (*iv*) mean swimming speed of return to the focal point (return speed). We used separate repeated measures analyses of variance (ANOVAs) for each of these (S-Plus 6 for Windows, Insightful Corporation, Seattle, Washington). This procedure treats subjects as blocks to account for variation among individuals. If coho and steelhead differed in their responses as velocity increased, we would expect to see a significant velocity × species interaction. Because the relationships between velocity and the dependent variables tested are of ecological interest, we also plot these data for each fish and provide separate regression equations for coho and steelhead for each of the factors.

## Results

### Prey capture probability

The effect of water velocity on prey capture probability was highly significant, but the effects of species and the interaction of velocity × species were not significant ($p$ = 0.05) (Table 1). Overall prey capture probability for both species was reduced from 65% to 25% with a water velocity increase from 29 to 55 cm·s$^{-1}$, with both species averaging nearly identical probabilities at these velocities (Fig. 2). The lack of a significant effect of species or of the velocity × species interaction suggests that neither the elevation nor the slope of the regression lines for coho and steelhead differ (Table 2, Fig. 2).

### 3D analysis: prey detection, prey interception, return to the focal point

The effect of water velocity on prey detection distance was also highly significant, but again the effects of species and velocity × species interaction were not significant (Table 1). Again the slopes and elevation of the regression lines did not differ (Table 2, Fig. 3*a*). Prey were detected throughout the detection volume rather than on the surface (i.e., at the reaction distance), and mean detection bearing increased with increasing velocity (Fig. 4). The reduction in detection distance was largely due to a reduction in the mean upstream ($x$ axis) distance rather than in the lateral ($y$ axis) or vertical ($z$ axis) distances (Fig. 5).

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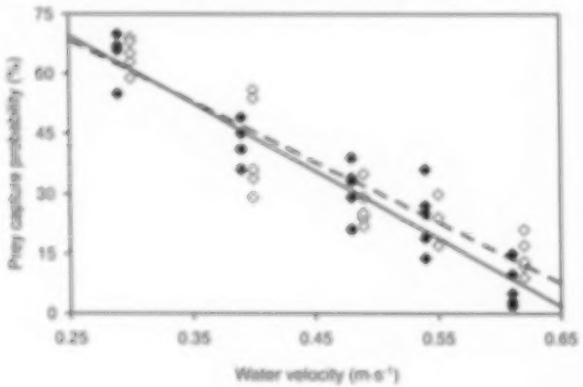
**Table 2.** Regression equations and $r^2$ values for prey capture characteristics of juvenile coho salmon (*Oncorhynchus kisutch*) and steelhead (sea-run rainbow trout, *Oncorhynchus mykiss irideus*) ($N = 5$ of each species).

| Regression *y* variable | Species | Regression equation | $r^2$ |
|---|---|---|---|
| No. of prey captures | Coho | $y = -169.2x + 112.0$ | 0.90 |
| | Steelhead | $y = -151.9x + 104.8$ | 0.85 |
| Prey detection distance (m) | Coho | $y = -0.25x + 0.38$ | 0.44 |
| | Steelhead | $y = -0.30x + 0.42$ | 0.69 |
| Interception speed ($m \cdot s^{-1}$) | Coho | $y = -0.07x + 0.41$ | 0.02 |
| | Steelhead | $y = -0.11x + 0.45$ | 0.09 |
| Return speed ($m \cdot s^{-1}$) | Coho | $y = 1.37x - 0.11$ | 0.93 |
| | Steelhead | $y = 1.39x - 0.13$ | 0.95 |

**Note:** Regression variable *x* in all equations is water velocity ($m \cdot s^{-1}$).

**Fig. 2.** Prey capture probability vs. water velocity for coho salmon (*Oncorhynchus kisutch*) (solid diamonds, solid line) and steelhead (sea-run rainbow trout, *Oncorhynchus mykiss irideus*) (open diamonds, broken line). Each data point represents the capture probability for one fish for a 25 min feeding trial ($N = 5$ of each species). Each fish was tested at each velocity, assigned in a random order. Steelhead data points are offset by +0.01 $m \cdot s^{-1}$ for visual clarity. Regression equations are found in Table 2.




Neither water velocity, species, nor the velocity × species interaction significantly effected prey interception speed (Table 1), again suggesting no difference between species (Table 2, Fig. 3*b*). At all velocities, coho and steelhead intercepted prey at close to their predicted maximum sustainable swimming speeds ($V_{max} = 0.41$ $m \cdot s^{-1}$), as calculated using equations for juvenile sockeye salmon (*Oncorhynchus nerka*) of the same size (Brett and Glass 1973) (Fig. 3*b*). The mean *x* coordinates for prey capture location were located further downstream with increasing velocity (Fig. 5). At the slowest velocity, fish of both species intercepted about an equal percentage of prey both upstream and downstream of the focal point; at faster velocities, nearly all prey were intercepted downstream of the focal point (Fig. 5). Capture probabilities declined nearly uniformly within the capture area (Fig. 6).

The effect of water velocity on return speed was highly significant, but the effects of species and the interaction of velocity × species were not significant (Table 1); again there was no difference between species in either the slope or elevation of the regression lines (Table 2, Fig. 3*c*). Fish returned to the focal point at approximately the same speed as the current until it exceeded their $V_{max}$, after which they exceeded current speed. At the faster velocities, fish tended to swim quickly to the substrate after a prey capture and then swim along the bottom back to the focal point.

## Discussion

Drift-feeding coho and steelhead appear to differ little in their response to increasing water velocity. Nearly equal prey capture probabilities, combined with similar detection distances and swimming speeds, suggest that both species use very similar search and capture methods while drift feeding. In a related series of experiments, we also found that juvenile coho and steelhead differ little in their responses to increases in water depth (Piccolo et al. 2007). It seems possible, therefore, that differential prey capture ability cannot explain velocity or depth selection by juvenile coho and steelhead. Other factors, either physical (e.g., temperature, light intensity) or biological (e.g., competition, prey capture costs, prey selectivity), may be responsible for habitat segregation between the species. This has been shown for other pairs of sympatric stream salmonids (Everest and Chapman 1972; Nakano et al. 1999), but field studies identifying the underlying mechanism for habitat selection by sympatric coho and steelhead is lacking. Because water velocity appears to have similar effects on prey detection and capture by both species, we focus the remainder of this discussion on the effects of velocity in general, which we anticipate may be similar for other species of juvenile drift-feeding salmonids.

The inverse relationship between water velocity and prey capture probability appears to be due to two factors: (*i*) a decrease in prey detection distance (i.e., faster-moving prey are detected closer to the fish) and (*ii*) a decrease in detection probability for any given prey within the potential detection area. The first of these has been reported for drift-feeding salmonids (Hill and Grossman 1993; O'Brien and Showalter 1993) and also for drift-feeding coral reef fish (Kiflawi and Genin 1997). In our experiments, detection distance decreased more in the upstream direction, whereas O'Brien and Showalter (1993) and Kiflawi and Genin (1997) reported a decrease in the lateral detection distance. The prey detection area has been described as a pie-shaped wedge projecting forward from the fish's focal point, delimited upstream by their detection distance and across-stream by the

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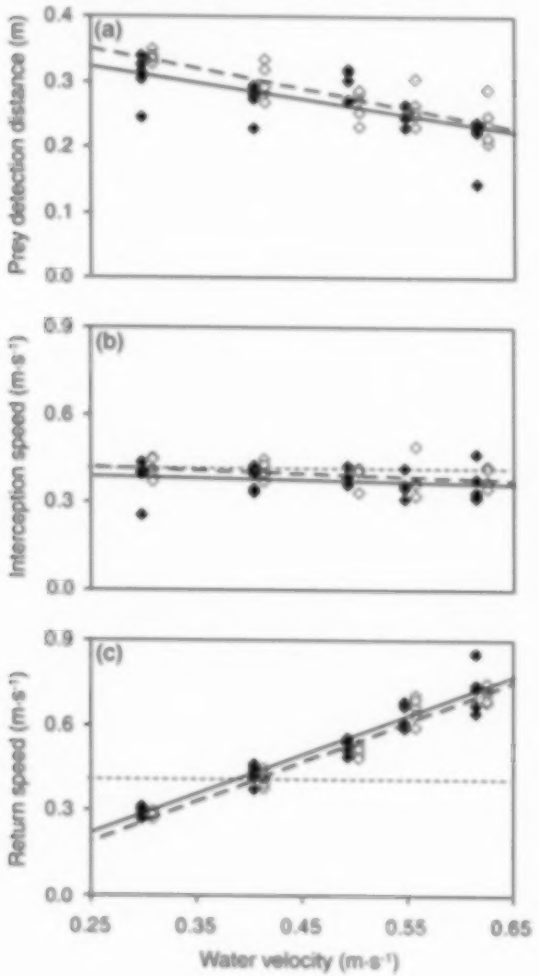
**Fig. 3.** Mean (*a*) prey detection distance, (*b*) interception speed, and (*c*) return speed vs. water velocity for coho (*Oncorhynchus kisutch*) (solid diamonds, solid lines) and steelhead (sea-run rainbow trout, *Oncorhynchus mykiss irideus*) (open diamonds, broken lines). Each data point represents the mean value of the *y* variable for one fish for a 25 min feeding trial ($N = 5$ of each species). The finely dashed horizontal lines in panels *b* and *c* are the predicted maximum sustainable swimming speeds for coho and steelhead. Steelhead data points are offset by +0.01 m·s$^{-1}$ for visual clarity. Regression equations are found in Table 2.




search angle (Hughes and Dill 1990; O'Brien and Showalter 1993; Kiflawi and Genin 1997). Our results show that the detection area may be reduced in an upstream rather than an across-stream direction, resulting in a shorter, not narrower, piece of pie. Whether the differences between our findings and those of O'Brien and Showalter (1993) and Kiflawi and Genin (1997) are due to fish species or size or to differences in experimental conditions is unknown. If fish are able to adjust the size and shape of their search area, they may be better able to adjust to changing environmental (e.g., stream discharge) or biological (e.g., presence of competitors) conditions.

Decreased prey detection probability within the capture area appears to be an important factor that limits prey capture success. Hughes et al. (2003) proposed that velocity-dependent prey detection limitations might be one explanation for their model's over-prediction of foraging rate in adult brown trout (*Salmo trutta*). Similarly, Kiflawi and Genin (1997) proposed that a velocity-dependent decline in prey detectability and (or) capture success within the foraging area (the area in which prey are both detected and captured) might be responsible for their model's over-prediction of foraging rates of drift-feeding coral reef fish at faster velocities. Our results — a lack of velocity-dependent narrowing of the detection area; prey detections throughout, rather than on the surface of, the detection area; and a uniform reduction in detections within this area — support this idea of velocity-dependent prey detection limitations. Because our fish searched an area of similar height and width at all velocites (i.e., the maximum detection distance declined little), the volume of water searched (i.e., search volume) increased nearly proportionally to water velocity. Searching a larger volume of water for faster-moving prey would almost certainly decrease the probability of detection if information-processing ability was limiting. Hughes et al. (2003) note that no exisiting model of prey detection can explain spatial variability in prey detection; our results show that search volume and prey speed need to be incoroporated into such models. Our experimental design, with known prey introduction locations and rates and variable water velocities, offers an effective means of testing prey detection models.

A velocity-dependent narrowing of the prey detection area has been an essential part of drift foraging models, used to predict the effects of water velocity on energy intake and consequently for predicting an optimum feeding velocity (Hughes and Dill 1990; Kiflawi and Genin 1997). To explain this narrowing, these models have assumed (*i*) that prey are detected at the fish's reaction distance, (*ii*) that prey are captured upstream of a line perpendicular to the fish's focal point, and (*iii*) a 100% capture probability on all energetically favorable prey. Our results and those of O'Brien and Showalter (1993) and Hughes et al. (2003) have shown this first assumption to be false. Although our maximum detection distance corresponds closely to the distance for coho of this size, as reported by Dunbrack and Dill (1984), the mean detection distance was less than the reaction distance, and it decreased with increasing water velocity. Our results also corraborate reseach that shows the second assumption to be false (Hughes et al. 2003), and further, they demonstrate that the downstream distance and the proportion of prey captured downstream of the focal point is velocity-dependent. Lastly, our results show the third assumption to be false, because prey capture probability within the foraging area never exceded 70%. This, coupled with the fact that we did not find a velocity-dependent narrowing of the foraging area as previously reported (O'Brien and Showlater 1993; Kiflawi and Genin 1997), may lend insight into why foraging models have successfully predicted habitat selection despite incorporating these false assumptions. It is possible that the additional prey detected and captured both more laterally and further downstream than the models allow represent an

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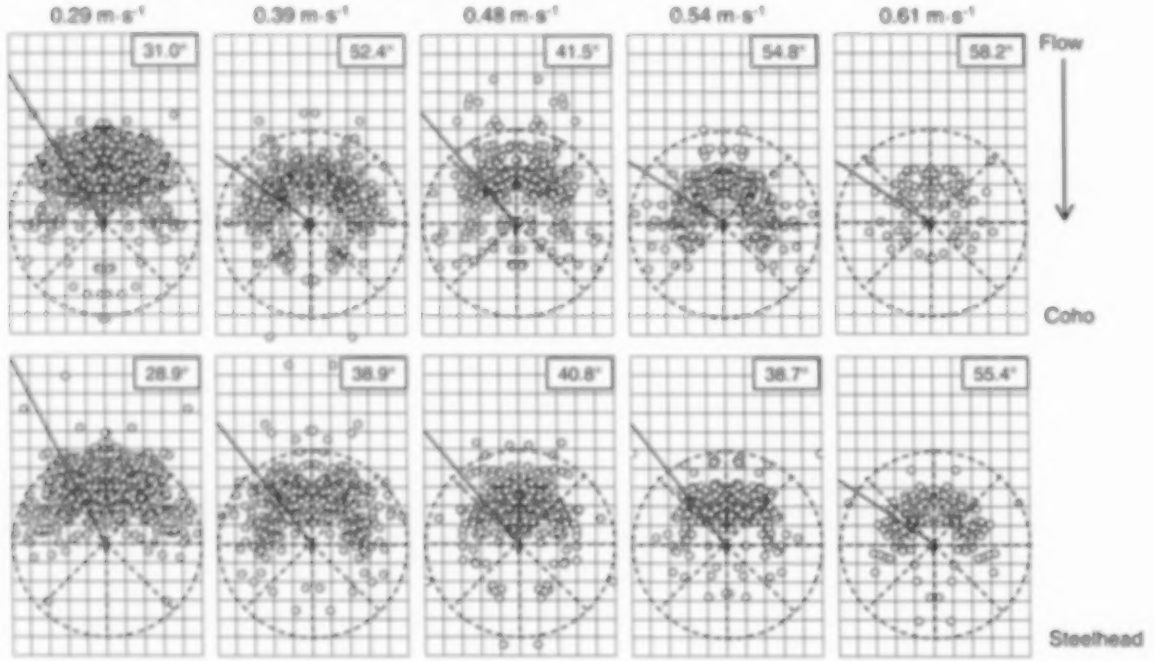
**Fig. 4.** Top view of prey detection locations (*x*,*y* coordinates) for coho (*Oncorhynchus kisutch*) (top) and steelhead (sea-run rainbow trout, *Oncorhynchus mykiss irideus*) (bottom) at five water velocities, listed at the top of the figure. Data are pooled for all fish ($N = 5$ of each species) tested at each velocity. Each circle represents one prey capture. Water flow is from top to bottom of figure. Solid lines to the left of the fish are mean prey detection angles (bearings in box) with 0° upstream and 180° downstream of fish. Detection locations have been rotated into the horizontal plane, retaining distance and bearing.




approximate trade-off for those prey within the foraging area that the models wrongly assume are captured.

Fish of both species intercepted prey at close to their predicted $V_{max}$ at all velocities. One explanation for this is that at $V_{max}$ fish should minimize their handling time while not aquiring oxygen debt as they would by swimming at burst speed (Puckett and Dill 1984). These results agree with Hughes et al.'s (2003) model assumption that fish should intercept prey at $V_{max}$. They differ from their results for adult brown trout, however, which tend to intercept prey at the same speed at which the prey drift (i.e., the same as water velocity). Because our fish did not increase interception speed at faster velocities, downstream displacement for prey captures increased as water velocities increased. Although this is mitigated somewhat by decreased prey detection distance at faster velocities, the net effect is a greater return distance as velocity increases.

Unlike interception speeds, return speeds were velocity dependent, with fish swimming at increasingly faster speeds at faster water velocities (again with no difference between species). At velocities less than $V_{max}$, fish returned to the focal point at the same speed as water velocity. At velocities faster than $V_{max}$, they swam faster than water velocity, thereby possibly incurring oxygen debt by burst swimming (Puckett and Dill 1984). There were velocity-dependent behavioural differences as well, with fish at slow velocities apparently searching for prey while returning to the focal point and fish at fast velocities burst-swimming towards the substrate and returning the remainder of the distance to the focal point along the velocity shelter of the substrate. Models of drift feeding have often disregarded the costs of prey capture as relatively unimportant (e.g., Hughes and Dill 1990; Hill and Grossman 1993). Our results suggest that return costs may be considerable if fish are foraging in areas of velocity greater than their $V_{max}$.

One important factor that we did not consider in this study is prey density (number of prey per unit volume of water) and its influence on prey encounter rate. In our experiments, we held prey encounter rate constant (4 prey·min$^{-1}$) to reduce the effects of increasing encounter rate on measurements of prey detecion and capture probability. This has the effect of reducing prey density, because as velocity increases, the volume of water that passes the fish's focal point increases while prey encounter rate remains constant. In natural streams, however, prey encounter rate is expected to increase proportionally to water velocity (Everest and Chapman 1972), and fish are expected to increase their capture rate until the time it takes to detect and capture one prey limits their ability to capture the next prey (termed the functional response; O'Brien et al. 2001). The prey encounter rate we used was well within the published foraing rates for drift-feeding salmonids (Biro et al. 1996; O'Brien et al. 2001), so it is unlikely that encounter rate limited capture probability even at our highest prey densities (i.e., the slowest velocities). Whether or not the benefits of the expected increase in prey encounter rate in faster water can

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**Fig. 5.** Front and side views of prey detection and prey capture locations for coho (*Oncorhynchus kisutch*) (left) and steelhead (sea-run rainbow trout, *Oncorhynchus mykiss irideus*) (right). Grid squares are 0.10 m × 0.10 m. Front view is the same for detection and capture locations; top side view in each panel is detection and bottom is capture. Arrows indicate mean $x$, $y$, $z$ axes detection and capture distances. Data are pooled for five of each species tested at each velocity. Each circle represents one prey capture.

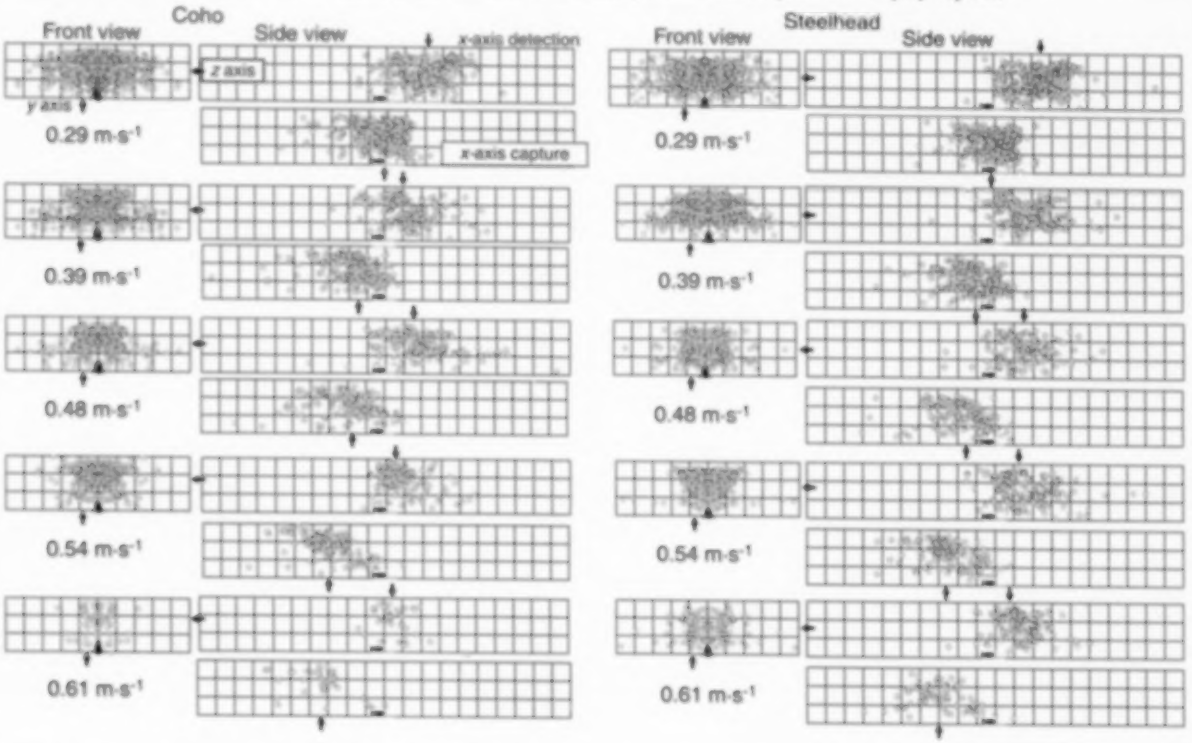
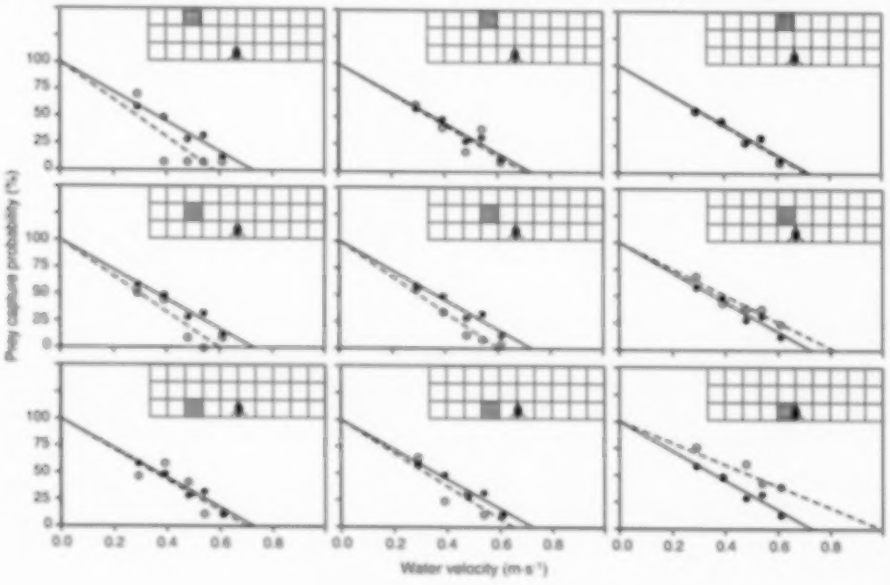



**Fig. 6.** Capture probability vs. water velocity for coho (*Oncorhynchus kisutch*) (solid circles, solid lines) and steelhead (sea-run rainbow trout, *Oncorhynchus mykiss irideus*) (open circles, broken lines) for each 0.10 m × 0.10 m square of the capture area shown by gray shading in the front view figure. Each data point represents the mean capture probability of five fish.

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outweigh the demonstrated reduction in capture probablity remains to be tested.

Our experiments were designed to isolate the effects of water velocity on drift-feeding salmonids. Our results corraborate and extend the findings of earlier research that suggested a negative relationship between water velocity and prey capture probablity for drift-feeding salmonids (Hill and Grossman 1993; O'Brien and Showalter 1993). We conducted our experiments over a wider range of velocities and with a greater number of replicates, and our 3D analyses are the first to clearly demonstrate both a decreased prey detection distance and a decline in capture probablity within the detection area. Although we attempted to simulate natural conditions in our stream tank, there are a number of factors that we did not address, but that are likely to influence prey detection and capture probabilities in natural streams. These include both physical (e.g., light intensity, temperature, water depth) and biological (e.g., competition, predation risk, prey size or density) factors. The interaction of these factors with water velocity should be considered if our results are to be incorporated into foraging models or applied to field studies.

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# Enriched stable isotope marking of juvenile golden perch (*Macquaria ambigua*) otoliths

**Andrew R. Munro, Bronwyn M. Gillanders, Travis S. Elsdon, David A. Crook, and Andrew C. Sanger**

**Abstract:** Stocking of native fish is a standard practice to aid in the recovery and enhancement of depleted populations. However, evaluating the effectiveness of these stocking programs has been hindered because of difficulty in distinguishing hatchery from wild fish, especially for species that are stocked as small, fragile fingerlings. Stable isotopes offer the potential to chemically mark fish with multiple marks that are distinct from each other and from natural signatures. Golden perch (*Macquaria ambigua*) fingerlings were reared in water enriched in $^{137}$Ba and combinations of $^{137}$Ba and $^{86}$Sr for various lengths of time. Ba and Sr isotopic ratios in the otoliths were determined using laser ablation inductively coupled plasma-mass spectrometry. Fish exposed to increased levels of $^{137}$Ba had lower $^{138}$Ba/$^{137}$Ba ratios in their otoliths relative to the natural ratio of control fish and were significantly different in fish exposed to at least 5 μg·L$^{-1}$ for 8 days or to 15 μg·L$^{-1}$ for 4 days. Furthermore, eight unique signatures were produced in fish reared in combinations of $^{137}$Ba (0–5 μg·L$^{-1}$) and $^{86}$Sr (0–100 μg·L$^{-1}$) for 24 days. Our results suggest that immersion in water enriched in specific stable isotopes could be an effective means of marking hatchery-reared fish for stock enhancement.

**Résumé :** L'empoissonnement de poissons indigènes est une pratique courante pour assurer la récupération et l'accroissement des populations épuisées. Cependant, l'évaluation de l'efficacité de ces programmes d'empoissonnement est entravée par la difficulté qu'il y a à distinguer les poissons de pisciculture des poissons sauvages, particulièrement chez les espèces qui sont ensemencées comme fretin fragile de petite taille. Les isotopes stables permettent de marquer chimiquement les poissons de signatures qui peuvent être distinguées les unes des autres et des signatures naturelles. Nous avons élevé des jeunes de la perche dorée (*Macquaria ambigua*) dans de l'eau enrichie de $^{137}$Ba ainsi que des combinaisons de $^{137}$Ba et de $^{86}$Sr pour diverses périodes de temps. Nous avons mesuré les rapports d'isotopes Ba et Sr dans les otolithes par spectrométrie de masse à couplage plasma inductif et ablation laser. Les poissons exposés à des concentrations élevées de $^{137}$Ba ont des rapports $^{138}$Ba/$^{137}$Ba plus bas dans leurs otolithes que ceux que l'on trouve naturellement chez les poissons témoins; les rapports diffèrent aussi significativement chez des poissons exposés à au moins 5 μg·L$^{-1}$ pendant 8 jours et chez d'autres exposés à 15 μg·L$^{-1}$ pendant 4 jours. De plus, il a été possible de produire huit signatures distinctes chez des poissons élevés dans des combinaisons de $^{137}$Ba (0–5 μg·L$^{-1}$) et de $^{86}$Sr (0–100 μg·L$^{-1}$) pendant 24 jours. Nos résultats indiquent que l'immersion dans de l'eau enrichie d'isotopes stables spécifiques pourrait être une méthode efficace pour marquer les poissons élevés en pisciculture lors d'opérations d'amélioration des stocks.

[Traduit par la Rédaction]

## Introduction

Marking and tagging fish is an essential tool for fisheries research and management. Identifying individual or groups of fish is important for assessing abundance, age and growth (including age validation), mortality, stock identity, movement and migration, stocking success, and contribution of different sources (stocked or wild) to mixed populations (McFarlane et al. 1990; Reinert et al. 1998). For example, over 45 million Pacific salmon (*Oncorhynchus* spp.) and steelhead (sea-run rainbow trout, *Oncorhynchus mykiss*) are coded-wire tagged annually in North America to assess hatchery contribution and productivity, allocation of harvest rights, establishment of escapement goals (i.e., fish that survived all fisheries and are part of the spawning population), and for general monitoring of the fisheries (Pacific States Marine Fisheries Committee 2006). Without tagging hatchery-reared fish, the fate of these fish and the effectiveness of stocking would remain unknown.

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A number of methods to mark or tag juvenile fish are available but few fully satisfy many of the basic criteria considered important for marking hatchery fish. Marks or tags should be inexpensive, easily applied with minimal handling of the fish, suitable for application to large numbers of small fish, retained for a reasonable amount of time, and easily detected. In addition, they should not be harmful or stressful to the fish or disrupt the hatchery routine (Ennevor and Beames 1993; Brown and Harris 1995). Furthermore, the marking method should consistently and reliably mark 100% of the fish. Physical tags, such as coded wire tags, have been shown to be an effective tagging method for small salmonids (Kaill et al. 1990; Peltz and Miller 1990; Munro et al. 2003) as well as native Australian fish (golden perch (*Macquaria ambigua*) and silver perch (*Bidyanus bidyanus*)) (Ingram 1993). However, some of the drawbacks of the coded wire tagging system include the variability in retention rates as a result of operator experience (Ingram 1993) and the cost of tagging and detection equipment. Consequently, coded wire tagging needs to be done on a large scale to be economically feasible (Nielsen 1992). Tagging fish individually is also labour intensive (Nielsen 1992); however, recent development of fully automated fish tagging and fin clipping systems reduce the labour involved with these methods. Otolith thermal marking is also a common marking technique. Like physical tags, thermal marking has drawbacks, which include limited tag period (between eyed-egg and fry stages) and loss of tag detection due to background increment noise (Volk 1999).

Chemical marking is a viable alternative to physical tags and thermal marking. The advantage of chemical marking is that large numbers of fish can be marked simultaneously with minimal handling. In addition, fish can be marked at any life-history stage, including egg and embryo (e.g., Dabrowski and Tsukamoto 1986; MacLellan and Fargo 1995; Eckmann 2003).

Chemical marking can be divided into two main categories: fluorescent compounds (i.e., visible marks) and elements. Marks made with fluorescent compounds (e.g., oxytetracycline and calcein) are known to be long-lasting (MacLellan and Fargo 1995; Negus and Tureson 2004). There are, however, problems associated with fluorescent marking, including excessive stress and mortality (Thomas et al. 1995), reduced mark detection with time (Dabrowski and Tsukamoto 1986; Reinert et al. 1998), and the need to adjust pH of the water to improve solubility of the compounds and buffer it from severe changes in pH (Butcher et al. 2003; van der Walt and Faragher 2003).

Elemental marking of otoliths is a potentially useful method for marking fish (Ennevor and Beames 1993; Brown and Harris 1995), with strontium being the most commonly used element for this purpose. The Sr:Ca ratios of fresh waters, however, are variable and can be as high or higher than saltwater (Kraus and Secor 2004). Therefore, one needs to be certain that the Sr mark cannot be mistaken for a natural signature. To ensure that the Sr:Ca mark is distinct from natural signatures, knowledge of the natural variation in the Sr:Ca that the fish may encounter is required. Given the variability of Sr:Ca in water (see Kraus and Secor 2004), large amounts of Sr may be required to produce a mark that is clearly artificial and cannot be mistaken for a natural signature. Other elements that naturally occur in low concentrations (e.g., rare earth elements) have had variable success in producing chemical marks in fish (see Behrens Yamada and Mulligan 1990; Ennevor and Beames 1993).

Stable isotopes offer an alternative to simple elemental or fluorescent marking of fish. Measurements of isotopic ratios in otoliths have primarily been limited to C, O, Sr, and S and have been used to investigate stock structure (e.g., Edmonds and Fletcher 1997; Bastow et al. 2002), trace the origin and movement of fish (e.g., Kennedy et al. 2002, 2005), and discriminate hatchery from wild fish (e.g., Weber et al. 2002). All of these studies, however, have relied upon natural variation in isotopic ratios. In this study, we investigate the use of enriched stable isotopes ($^{137}$Ba and $^{86}$Sr) to create marks that are unequivocally artificial and cannot be mistaken for a natural signature.

The objectives of this study were to investigate the feasibility of marking otoliths with elements enriched in specific stable isotopes and to determine whether multiple unique marks could be induced using combinations of enriched isotopes, which can then be used as batch marks. In Australia, over three million native fish are stocked in the Murray–Darling Basin (MDB) annually with the primary aims of enhancing recreational fisheries and native species conservation. However, little is known about the fate of these stocked fish or their interactions with wild populations because there is not an established marking program with a suitable marking method. Many of the fish used for stocking in the MDB are produced by private hatcheries and stocked by local angling and community groups as fingerlings (1–2 months old, 30–50 mm total length). In addition, hatchery operators prefer to minimize the handling of the fish destined for stocking, which are reared in earthen ponds and quarantined in the hatchery for 24–48 h before being released.

## Materials and methods

### Experimental design

Juvenile golden perch, about 30 mm total length, were obtained from the hatchery operated by New South Wales Department of Primary Industries at Narrandera, NSW, Australia, and transported to the University of Adelaide, SA, Australia, where all of the experiments were conducted. Prior to transportation, fish were immersed in alizarin complexone (ALC) to mark the otoliths (see van der Walt and Faragher 2003) so that pre- and post-experimental growth could be identified in subsequent analyses. This marking was done at the hatchery 14 days before starting the experiments. After transportation, the fish were allowed to acclimate for 10 days in a 250 L tank. The water used throughout these experiments was collected from wells located at the South Australian Research and Development Institute, Aquatic Sciences Division, and was stored in a 2000 L indoor tank. Fish were fed live oligochaete blackworms to satiation twice daily. After acclimatization, 10 fish were randomly assigned to 5 L tanks for the experiments. The experimental treatments and controls were randomly split between two constant-temperature rooms, which were maintained at 21–22 °C (similar to water temperatures experienced by the fish at the source hatchery) and a 12 h light:12 h dark cycle (similar to the 12–14 h natural daylight

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fish receive at the source hatchery at that time of year). To maintain water quality in these closed systems, 50% of the water was changed every second day, and the solid waste was siphoned from the bottom of the tank.

### *Experiment 1: concentration and immersion time*

The aim of the first experiment was to test the effect of concentration and immersion time on the incorporation of enriched $^{137}$Ba into the sagittal otoliths. An enriched $^{137}$Ba solution of known concentration was made by dissolving $BaCO_3$ enriched in $^{137}$Ba (81.9% $^{137}$Ba and 17.4% $^{138}$Ba; Oak Ridge National Laboratories, Oak Ridge, Tennessee, USA) in a small amount of ultrapure water and concentrated HCl, then diluted to a given volume once the reaction had ceased and all of the carbonate had dissolved. The appropriate amount of solution was then pipetted into each treatment tank to give the desired final concentration. The treatments for this experiment consisted of three enriched $^{137}$Ba concentrations (1, 5, and 15 $\mu g \cdot L^{-1}$) and four immersion times (1, 4, 8, and 24 days) in an orthogonal two-factor design. Two replicate tanks for each treatment were used to control for possible tank effects. To maintain the desired isotopic ratios during the experiment, the treatment tanks were spiked with appropriate amounts of enriched $^{137}$Ba solution after each water change. The control treatment consisted of two tanks with fish reared in ambient water for the length of the experiment. After the specified immersion time (1, 4, or 8 days), the fish were returned to ambient water until the end of the experiment at 24 days; one treatment was reared for 24 days in enriched $^{137}$Ba.

### *Experiment 2: unique batch marks*

The aim of the second experiment was to determine if multiple unique marks could be induced in otoliths using combinations of multiple enriched isotopes ($^{137}$Ba and $^{86}$Sr). An enriched $^{86}$Sr solution for spiking the treatments was made by dissolving $SrCO_3$ enriched in $^{86}$Sr (96.8% $^{86}$Sr and 2.4% $^{88}$Sr; Oak Ridge National Laboratories, Oak Ridge, Tennessee, USA) in a small amount of ultrapure water and concentrated HCl, in the same manner as described for $BaCO_3$. The same Ba solution was used as in the previous experiment. At the start of the experiment, treatments were spiked with the appropriate amounts of enriched $^{137}$Ba and $^{86}$Sr. Treatments for this experiment consisted of all combinations of enriched $^{137}$Ba (0, 1, and 5 $\mu g \cdot L^{-1}$) and enriched $^{86}$Sr (0, 25, and 100 $\mu g \cdot L^{-1}$) for a total of eight treatments, plus control. This experiment was run for two different immersion times (1 and 24 days). Two replicate tanks for each treatment and immersion time combination were used to control for possible tank effects. To maintain the desired isotopic ratios during the experiment, the treatment tanks were spiked with appropriate amounts of enriched $^{137}$Ba and $^{86}$Sr solutions after each water change. The fish in the 1-day treatments were returned to ambient water after 24 h and reared until the end of the experiment at 24 days.

### Otolith preparation

At the end of the experiments, the fish were killed by immersion in an ice slurry and immediately frozen until the sagittal otoliths were extracted. Upon extraction, the otoliths were rinsed thoroughly with ultrapure water to remove adhering tissue, dried in a laminar flow hood, and stored in microcentrifuge tubes. The left otoliths were selected for analysis, although systematic differences between the left and right otoliths are not expected with normal otoliths. Otoliths were embedded in two-part epoxy (Struers Epofix), which had been spiked with 40 ppm indium to allow for discrimination between the otolith and the epoxy upon analysis. Otoliths were sectioned transversely using a low-speed saw (Buehler Isomet). The sections were then polished with 9 µm lapping film, followed by 3 µm lapping film until they were about 250–300 µm thick (see Elsdon and Gillanders 2002). Sections were rinsed with ultrapure water between each stage to remove any surface contamination and allowed to dry in a laminar flow hood. The otolith sections of three fish from each treatment tank were randomly selected and mounted on glass microscope slides with thermoplastic glue (CrystalBond 509) that had also been spiked with indium. Prepared sample slides were then sonicated in ultrapure water for 5 min and allowed to dry for 24 h in a laminar flow hood. Slides were stored individually in sealed plastic bags until analysed.

**Table 1.** Details of the operating parameters of the New Wave Nd Yag 213 nm UV laser and Agilent 7500cs inductively coupled plasma-mass spectrometer (ICP-MS) used to analyse the otoliths.

| Parameter | Description |
|---|---|
| **Laser** | |
| Wavelength | 213 nm |
| Mode | Q-switched |
| Frequency | 5 Hz |
| Spot size | 30 µm |
| Laser power | 65% |
| Beam energy | 0.1–0.15 mJ |
| Laser scan rate | 1 $\mu m \cdot s^{-1}$ |
| Carrier gas | Ar (0.7–0.92 $L \cdot min^{-1}$) |
| **ICP-MS** | |
| Optional gas | He (55–60%) |
| Cone | Pt |
| Dwell times | $^{137}$Ba and $^{138}$Ba (300 ms) |
| | $^{86}$Sr and $^{88}$Sr (200 ms) |
| Detection modes | Pulse and analogue |

### Otolith isotope analyses

Otoliths were analysed with a New Wave Nd Yag 213 nm UV laser operated in Q-switch mode connected to an Agilent 7500cs inductively coupled plasma-mass spectrometer (ICP-MS). Operating conditions of the laser and mass spectrometer are provided in Table 1. Laser profiles across the growth axis were done for each otolith starting 245 µm in from the edge out to the edge, which captured all growth during the experiment plus some pre-experiment growth (Fig. 1). This distance was determined on a subset of otoliths by measuring the distance from the edge to the ALC mark that had been created 14 days prior to the start of the experiments and adding an additional 10 µm onto the largest value.

A reference standard (NIST 612, National Institute of Standards and Technology, Gaithersburg, Maryland) was

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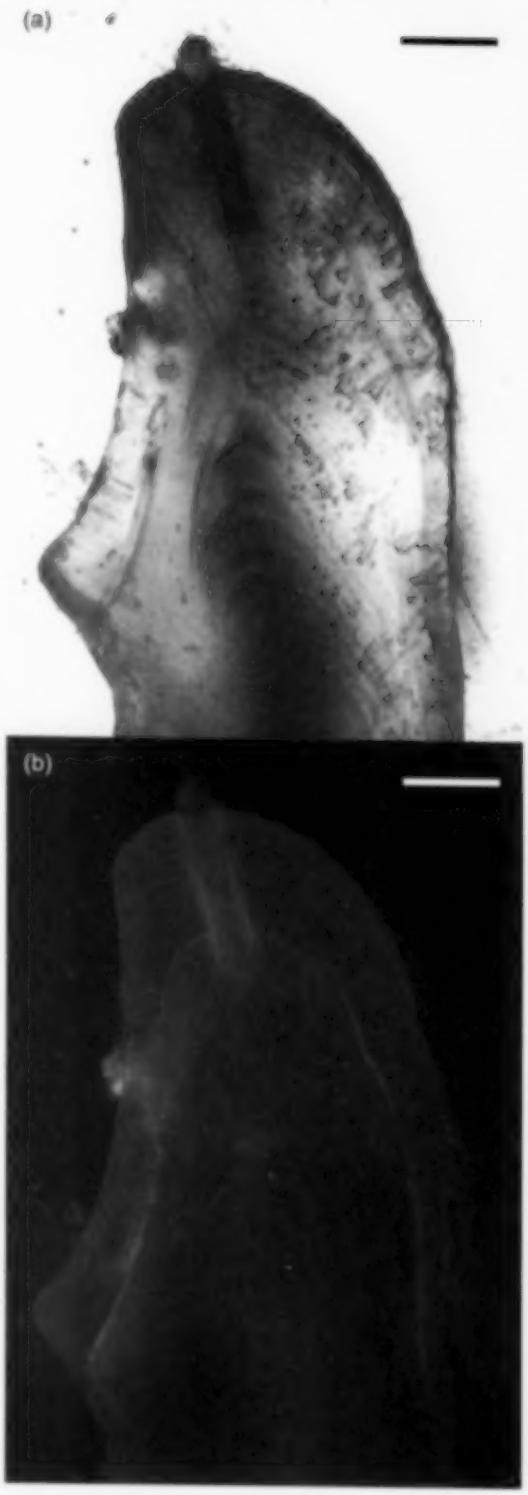


**Fig. 1.** Laser ablation inductively coupled plasma-mass spectrometry was used to measure Ba isotopic ratios from profiles across the growth axis of golden perch (*Macquaria ambigua*) otoliths sectioned through the nucleus. (*a*) Light photomicrograph showing profile line. (*b*) Fluorescence photomicrograph showing profile line and alizarin mark made 14 days prior to the start of the experiment. Scale bar = 0.1 mm.

analysed at the beginning and end of each session and periodically throughout the session to correct for mass bias and machine drift. It was assumed that the relative abundance of the isotopes of interest in the standard were the same as the relative natural abundances of $^{138}Ba/^{137}Ba$ and $^{88}Sr/^{86}Sr$ (i.e., 6.38 and 8.38, respectively) based on the International Union of Pure and Applied Chemistry (IUPAC) values of isotope abundances (Rosman and Taylor 1998). Correction factors for each session were then determined by plotting the measured isotopic ratios in the standard against time of analysis and fitting a regression model (linear or quadratic depending on best fit). The fitted model was then used to estimate the predicted isotopic ratio at the start of each sample, and the correction factor was calculated by dividing the predicted isotopic ratio by the expected natural ratio. The blank-subtracted abundances were used to calculate the isotopic ratios for the samples, which were then adjusted by the correction factor. The data were smoothed using a six-point running mean to remove some of the noise (similar to Sinclair et al. 1998). The minimum value of the smoothed data was then used as the isotopic value for that sample and for all analyses. The minimum value was used because it was expected that if the altered isotopic ratio of the water was reflected in the otolith, the ratio in the otolith would be lower than the natural ratios (the isotope in the denominator was enriched for both Ba and Sr).

**Data analyses**

The effect of concentration and immersion time on $^{138}Ba/^{137}Ba$ in otoliths of juvenile golden perch (experiment 1) was examined using a three-factor analysis of variance (ANOVA), with concentration and immersion time treated as fixed factors and tank (nested within the concentration × immersion interaction term) as a random factor. Data were not transformed because Cochran's test for homogeneity of variance indicated that variances were homogeneous ($P > 0.05$). Dunnett's multiple comparison procedure for comparing several treatments with a control (Dunnett 1955) was used to test which combination of concentration and immersion time significantly altered natural ratios. A one-sided test was used because the ratios were expected to be lower that the natural ratios. Mark success was determined by setting a successful mark criterion of 5.61, which was the mean $^{138}Ba/^{137}Ba$ ratio of the control treatment minus two standard deviations. Each fish was compared with this value, and if $^{138}Ba/^{137}Ba$ of an individual was less than 5.61, it was deemed successfully marked.

The ability to create unique marks using combinations of enriched $^{137}Ba$ and $^{88}Sr$ (experiment 2) was analysed using permutational multivariate analysis of variance (PERMANOVA, Anderson 2005), where each unique combination of enriched $^{137}Ba$ and $^{88}Sr$, as well as controls, were treated as

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separate levels in a fixed main factor. Replicate tanks were nested within the treatment level effect as a random effect. To further test the ability to discriminate among the marks, linear discriminant function analysis of the data were done using SPSS version 11.5 (SPSS Inc., Chicago, Illinois, USA). Cross-validation of the data was done to test the discriminant function model and determine the percentage of correct classification.

## Results

### Experiment 1: concentration and immersion time

Juvenile golden perch reared in water spiked with enriched $^{137}$Ba showed altered $^{138}$Ba/$^{137}$Ba ratios in their otoliths compared with fish reared in ambient water (control fish). The $^{138}$Ba/$^{137}$Ba ratio remained relatively constant along the growth axis of the otoliths of fish from the control group and was similar to the expected natural ratio value (Fig. 2*a*). Fish that were exposed to elevated $^{137}$Ba for 1 day typically showed only a slight decline in the isotopic ratio along the otolith profile, with a return to natural levels shortly after the fish was returned to ambient water (Fig. 2*b*). Longer exposure to altered Ba isotopic ratios resulted in more pronounced declines in $^{138}$Ba/$^{137}$Ba in the otolith profile (Figs. 2*c* and 2*d*). The isotopic ratio in the otolith reached equilibrium with the isotopically enriched water between 8 and 24 days of exposure (Figs. 2*d* and 2*e*).

Otolith $^{138}$Ba/$^{137}$Ba ratios were significantly different among fish exposed to different levels of enriched $^{137}$Ba for different lengths of time (Table 2, Fig. 3). Because the minimum values along the transect were used for each sample, the $^{138}$Ba/$^{137}$Ba ratios of the control fish were slightly lower than the expected natural isotopic ratio (6.06 vs. 6.38). There was a general decrease in $^{138}$Ba/$^{137}$Ba with increasing amount of enriched $^{137}$Ba added to the rearing water and with the length of immersion. At the lowest spiking levels (i.e., 1 μg·L$^{-1}$), a significant change in $^{138}$Ba/$^{137}$Ba was observed only in the 24-day treatments ($t$ = 2.79, $k$ treatments (excluding controls) = 12, df = 52, $P$ = 0.04), which had a mean ratio of 5.35 (Table 3). With an increase in spiking level to 5 μg·L$^{-1}$, both the 8- and 24-day treatments were different than the controls ($t$ = 4.77, $k$ = 12, df = 52, $P$ = 0.0001 and $t$ = 5.34, $k$ = 12, df = 52, $P$ < 0.0001, respectively), with respective mean ratios of 4.84 and 4.70. At a spiking dose of 15 μg·L$^{-1}$, mean $^{138}$Ba/$^{137}$Ba in the otoliths of the 4-, 8-, and 24-day treatments (5.19, 3.62, and 2.82, respectively) were different than the controls ($t$ = 3.42, $P$ < 0.0001; $t$ = 9.56, $P$ < 0.0001; $t$ = 12.71, $P$ < 0.0001, repsectively) (Fig. 3). Mark success improved with increasing concentration and exposure time (Table 3). At 5 μg·L$^{-1}$, 83% of the fish reared for 8 days in isotopically altered water were successfully marked, whereas there was 100% mark success for the 24-day treatment. At 15 μg·L$^{-1}$, there was 83% mark success in the 4-day treatment and 100% in both the 8- and 24-day treatments. Mark success for all other treatments ranged from 0% to 67% (Table 3).

### Experiment 2: unique batch marks

Immersion of juvenile golden perch in various combinations of enriched $^{137}$Ba and $^{86}$Sr at various concentrations in an effort to induce unique marks in the otoliths of juvenile golden perch had variable success. There was no discernable separation among the different combination levels or the controls for the fish that were immersed for only 1 day (Fig. 4*a*). There was, however, a significant difference in the otolith isotopic ratios of the golden perch in the 24-day treatment (Table 4, Fig. 4*b*). Pairwise a posteriori comparisons indicated that the eight combinations, plus controls, were all significantly different from each other except for three treatment combinations, which were marginally nonsignificant (1 and 5 μg $^{137}$Ba·L$^{-1}$ in combination with 0 μg $^{86}$Sr·L$^{-1}$ ($P$ = 0.0662), 0 and 1 μg $^{137}$Ba·L$^{-1}$ in combination with 25 μg $^{86}$Sr·L$^{-1}$ ($P$ = 0.0585), and 0 and 1 μg $^{137}$Ba·L$^{-1}$ in combination with 100 μg $^{86}$Sr·L$^{-1}$ ($P$ = 0.0571)). Linear discriminant function analysis was able to discriminate among the treatment groups. Overall, the cross-validation analysis correctly reclassified 96.3% of the fish. Two fish

**Fig. 2.** The effect of exposure time on duration on $^{138}$Ba/$^{137}$Ba ratios in otoliths of juvenile golden perch (*Macquaria ambigua*) reared in water spiked with enriched $^{137}$Ba at 15 μg·L$^{-1}$: (*a*) control fish (ambient Ba), (*b*) 1-day exposure, (*c*) 4-day exposure, (*d*) 8-day exposure, (*e*) 24-day exposure. Ratios are plotted as smooth six-point moving averages. Broken line indicates natural $^{138}$Ba/$^{137}$Ba ratio. Note that even though laser transects started 245 μm in from the otolith edge, the *x* axes in these examples range from 140 to 0 μm from the edge, which is sufficient to capture the entire experimental period and a small portion of pre-experimental growth in the otolith.

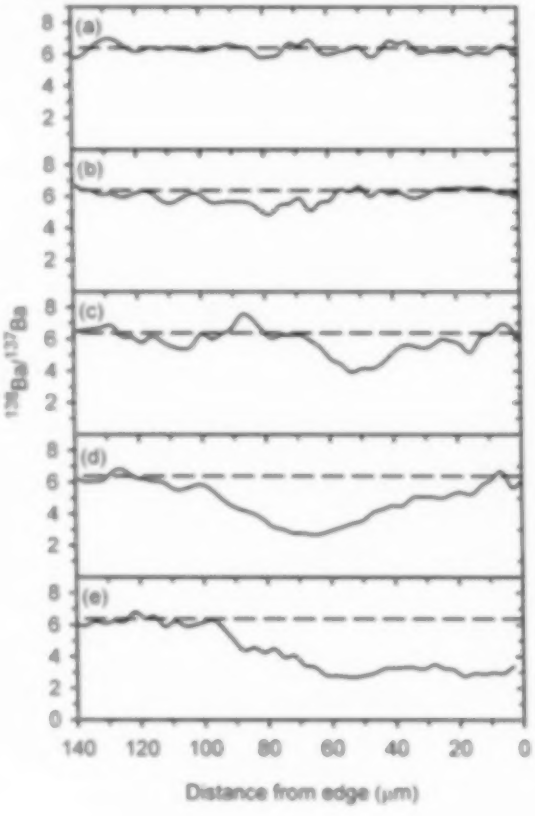


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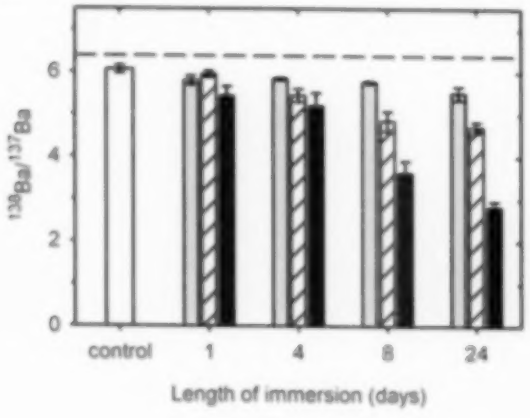
**Table 2.** Analysis of variance comparing $^{138}Ba/^{137}Ba$ ratios in the otoliths of juvenile golden perch (*Macquaria ambigua*) reared at different concentrations of enriched $^{137}Ba$ (1, 5, and 15 $\mu g \cdot L^{-1}$) for various lengths of time (1, 4, 8, and 24 days).

| Source | df | SS | MS | *F* | *P* >*F* |
|---|---|---|---|---|---|
| Concentration | 2 | 26.4890 | 13.2445 | 130.87 | <0.0001 |
| Time | 3 | 22.5060 | 7.5020 | 74.13 | <0.0001 |
| Concentration × Time | 6 | 12.2096 | 2.0349 | 20.11 | <0.0001 |
| Tank(Concentration × Time) | 12 | 1.2147 | 0.1012 | 0.47 | 0.9225 |
| Residuals | 48 | 10.3341 | 0.2153 | | |

**Note:** Cochran's test failed to reject the null hypothesis of homogeneity of variance among groups. *df*, degrees of freedom; SS, sum of squares; MS, mean square.

**Fig. 3.** Comparison of mean (±standard error) $^{138}Ba/^{137}Ba$ ratio in otoliths of juvenile golden perch (*Macquaria ambigua*) reared in water spiked with 1 (gray bars), 5 (hatched bars), and 15 $\mu g \cdot L^{-1}$ (solid bars) of enriched $^{137}Ba$ for 1, 4, 8, and 24 days. Controls are depicted by the open bar. The broken line indicates natural $^{138}Ba/^{137}Ba$ ratio.




were misclassified. One fish from the 1 $\mu g$ $^{137}Ba \cdot L^{-1}$ – 0 $\mu g$ $^{86}Sr \cdot L^{-1}$ treatment group was classified as coming from the control group (0 $\mu g$ $^{137}Ba \cdot L^{-1}$ – 0 $\mu g$ $^{86}Sr \cdot L^{-1}$). The other fish from the 5 $\mu g$ $^{137}Ba \cdot L^{-1}$ – 0 $\mu g$ $^{86}Sr \cdot L^{-1}$ treatment group was classified as coming from the 1 $\mu g$ $^{137}Ba \cdot L^{-1}$ – 0 $\mu g$ $^{86}Sr \cdot L^{-1}$ treatment group. Individuals from the remaining groups were 100% correctly classified.

## Discussion

These experiments demonstrate that both the Ba and Sr isotopic ratios in juvenile golden perch otoliths can be altered by rearing the fish in water spiked with enriched $^{137}Ba$ and $^{86}Sr$. In the first experiment, the results indicated that both spiking level of the enriched isotopes (i.e., $^{137}Ba$) and the immersion time influenced the $^{138}Ba/^{137}Ba$ ratio in the otolith. We were able to produce a detectable mark in the otoliths in as little as 4 days at concentrations of 15 $\mu g \cdot L^{-1}$ of enriched $^{137}Ba$. The isotopic ratio in the otolith reached equilibrium with the water between 8 and 24 days. In the second experiment, both Ba and Sr isotopic ratios were altered simultaneously to create unique marks within the otolith. Although immersion for 1 day at the concentrations used did not significantly alter the isotopic ratios, we were able to create several unique batch marks in the otoliths when the fish were reared for 24 days. Similar to this study, Walther and Thorrold (2006) altered the Ba and Sr isotopic ratios in the otoliths of mummichog (*Fundulus heteroclitus*) by rearing them in water spiked with 5 $\mu g \cdot L^{-1}$ of enriched $^{137}Ba$ and 100 $\mu g \cdot L^{-1}$ enriched $^{86}Sr$ for 70 days, although marking was not the purpose of their study.

There are several advantages of using enriched isotopes for marking the otoliths of juvenile fish. First, a distinct mark that cannot be mistaken for a natural signature can easily be produced. Unlike elemental markers, one does not need to be concerned about wild fish having similar signatures because it can be confidently assumed that all fish not exposed to the enriched isotopes would have natural stable isotopic abundances. It is advised, however, to first measure the isotopic ratios in unmarked fish to determine natural variation in the ratio and instrument measurement error. Second, the marking procedure is relatively stress free. Unlike physical tags, the fish do not need to be handled individually. Also, relatively low concentrations of these enriched isotopes are required to produce a mark, compared with fluorescent chemical and elemental markers. For example, the fluorescent chemical marker ALC is typically used in concentrations of 25–220 $mg \cdot L^{-1}$ to mark otoliths (Wilson 1995). The most commonly used elemental marker is Sr and concentrations of 1000 $mg \cdot L^{-1}$ have been found to produce distinctive marks in both golden perch otoliths (Brown and Harris 1995) and otoliths of sockeye salmon (*Oncorhynchus nerka*) (Oxman et al. 2003). We were able to produce shifts in the isotopic ratios using concentrations as low as 1 $\mu g \cdot L^{-1}$ of enriched $^{137}Ba$ and 25 $\mu g \cdot L^{-1}$ of enriched $^{86}Sr$ (24-day exposures). Third, isotopic marking (like elemental and chemical marking) can be applied to any life stage. In this study, fish were marked as fingerlings at the typical stocking size (~30 mm) and age (~6 weeks). Alternatively, there is the potential to mark fish at the larval stage. For example, 1- to 10-day-old larval walleye (*Sander vitreus*) have been successfully marked with fluorescent compounds (Brooks et al. 1994), suggesting that marking with stable isotopes should be feasible at this life stage. The general procedure for rearing golden perch larvae in hatcheries is to incubate the eggs in closed, aerated systems at densities of 125–250 $eggs \cdot L^{-1}$ (Rowland 1986). The larvae hatch in about 32 h (at 25 °C) and are maintained in these closed systems until they have absorbed their yolk and begin exogenous feeding (about 5 days), at which point they are stocked into earthen ponds for rearing up to stocking size. Isotopically marking the fish during the 5 days between hatching and commencement of

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**Table 3.** Summary table of mean $^{138}Ba/^{137}Ba$ ratios (standard deviations in parentheses) from experiment 1, Dunnett's multiple comparison procedure, and marking success (% marked) for different concentrations of enriched $^{137}Ba$ and exposure times.

| Concentration ($\mu g \cdot L^{-1}$) | Exposure time (days) | Mean $^{138}Ba/^{137}Ba$ | $t$ | $P > t$ | % marked |
|---|---|---|---|---|---|
| 0 (control) | 24 | 6.06 (0.23) | — | — | — |
| 1 | 1 | 5.80 (0.27) | 1.014 | 0.927 | 17 |
| | 4 | 5.84 (0.07) | 0.855 | 0.977 | 0 |
| | 8 | 5.76 (0.08) | 1.178 | 0.844 | 0 |
| | 24 | 5.35 (0.26) | 2.786 | 0.043 | 50 |
| 5 | 1 | 5.95 (0.18) | 0.441 | 0.999 | 0 |
| | 4 | 5.44 (0.38) | 2.418 | 0.110 | 50 |
| | 8 | 4.84 (0.56) | 4.771 | 0.0001 | 83 |
| | 24 | 4.70 (0.30) | 5.344 | <0.0001 | 100 |
| 15 | 1 | 5.44 (0.56) | 2.451 | 0.102 | 67 |
| | 4 | 5.19 (0.78) | 3.420 | 0.007 | 83 |
| | 8 | 3.62 (0.69) | 9.560 | <0.0001 | 100 |
| | 24 | 2.82 (0.33) | 12.710 | <0.0001 | 100 |

**Note:** Dunnett's test statistic ($t$) and $P$ values are based on 12 treatment groups plus the control, and 12 degrees of freedom for a one-tailed test. A mark was deemed successful if it was less than 5.61 (i.e., mean $^{138}Ba/^{137}Ba$ of the controls minus two standard deviations). Six otoliths were analysed for each treatment.

exogenous feeding would be ideal because the fish are being held in closed systems during this period; therefore, marking can easily be incorporated into routine production procedures. In addition, because the fish are smaller (~5 mm at hatching) and are held at higher densities, less volume of water would need to be enriched, and therefore less enriched isotopes would be needed, thus reducing the cost of marking.

The eggs and larvae of silver perch develop similarly to golden perch, and culture procedures are also similar (Rowland 1986); therefore, it is likely that silver perch could be marked in the same manner. In fact, marking at this stage would be suitable for any fish that are cultured using comparable methods (e.g., walleye (Harding et al. 1992) and red drum (*Sciaenops ocellatus*) (Davis 1990)).

The isotope measurement methods used in this study differ from standard otolith isotope analyses. Most isotopic analyses require extremely accurate analysis techniques, such as thermal ionization mass spectrometry (TIMS) (Kennedy et al. 2000). Instruments used to measure natural isotopic ratios are typically solution-based techniques (i.e., the samples need to be dissolved) and are therefore not suitable for fish that have only had a small portion of their otolith marked. The spatial and thus temporal information is averaged over the otolith, and the altered ratio, representing the isotope mark, can be swamped by the natural signal. Because the ratios in the otoliths are being shifted so drastically (1+ units), the high level of accuracy of solution-based instruments is not required. As demonstrated by this study and others (Thorrold et al. 2006; Walther and Thorrold 2006), standard laser ablation inductively coupled plasma–mass spectrometry (LA-ICP-MS) instruments fitted with quadrupole or magnetic sector ion detectors are sufficiently accurate for measuring such large differences in isotopic ratios, with the added benefit of being able to analyse specific areas within the otolith corresponding to different times within the fish's life. A new generation of LA-ICP-MS instruments, fitted with multicollector ion detectors, combine the accuracy of TIMS with the solid sample analysis capabilities of laser ablation and could be used to detect even smaller shifts in isotopic ratios for heavier elements such as Sr and Ba (e.g., Woodhead et al. 2005).

In these experiments, we used enriched $^{137}Ba$ and $^{86}Sr$ and demonstrated that with different concentrations of these two isotopes we could produce eight unique marks in the otoliths of golden perch. The isotope marks produced by spiking correspond to theoretical values based on mixing curves and calculations. Other enriched stable isotopes of Ba and Sr and other elements are commercially available and could potentially be used to produce many unique isotopic signatures in the otoliths of fish. Three other stable isotopes of Ba are available ($^{135}Ba$, $^{136}Ba$, and $^{138}Ba$), meaning that up to 15 different marks could be produced using just combinations of enriched Ba isotopes (Thorrold et al. 2006). Other enriched isotopes include strontium ($^{84}Sr$, $^{86}Sr$, $^{87}Sr$, and $^{88}Sr$), lithium ($^{6}Li$ and $^{7}Li$) and magnesium ($^{24}Mg$, $^{25}Mg$, and $^{26}Mg$), which would yield over 1000 unique marks if no more than four isotopes were used for a given mark. Although the relation between the incorporation of Mg and Li into otoliths and the concentration of elements in the water is not known (unlike elements such as Sr, Ba, and Mn; see Elsdon and Gillanders 2003), enriched isotopes of these elements may be useful markers and thus deserve further investigation.

The cost of marking and retrieving the marks is always a consideration when planning implementation on a large scale. While enriched $^{137}Ba$ and $^{86}Sr$ are expensive (US$4.36 and US$11.25 per milligram of element, respectively), the overall cost of marking fish is relatively low. Using our results as a guide, we estimate that it would cost US$9.80 to mark 1000 fish with enriched $^{137}Ba$ (4 days with 50% water change at 15 $\mu g \cdot L^{-1}$ and 10 fish$\cdot L^{-1}$) and US$42.00 to mark 1000 fish with enriched $^{86}Sr$ (4 days with 50% water change at 25 $\mu g \cdot L^{-1}$ and 10 fish$\cdot L^{-1}$). Retrieving the mark is more

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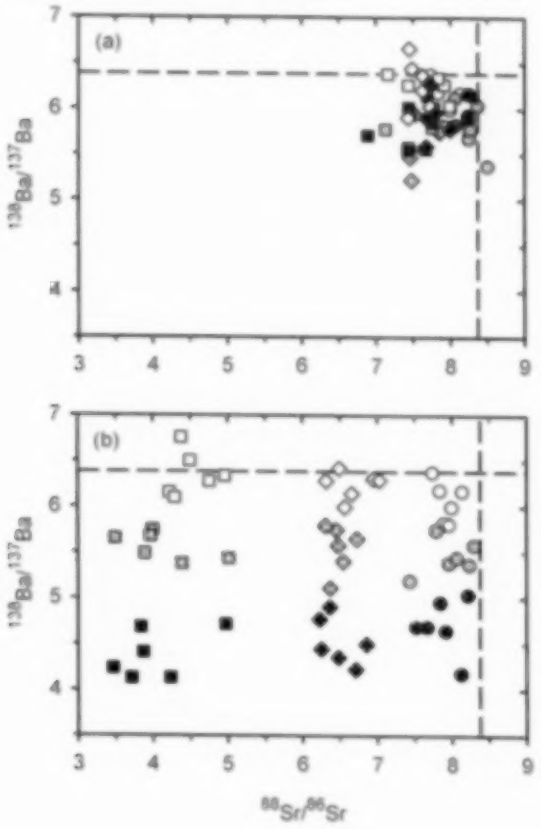
**Table 4.** Permutational multivariate analysis of variance comparing $^{138}Ba/^{137}Ba$ and $^{88}Sr/^{86}Sr$ ratios in the otoliths of juvenile golden perch (*Macquaria ambigua*) reared in various combinations of enriched $^{137}Ba$ (0.1, and 5 $\mu g \cdot L^{-1}$) and enriched $^{86}Sr$ (0, 25, and 100 $\mu g \cdot L^{-1}$) concentrations for 24 days.

| Source | *df* | SS | MS | *F* | P >*F* |
|---|---|---|---|---|---|
| Enriched $^{137}Ba$ and $^{86}Sr$ treatment | 8 | 153.3257 | 19.1675 | 102.69 | 0.0001 |
| Tank(Group) | 9 | 1.6797 | 0.1866 | 1.19 | 0.3123 |
| Residuals | 36 | 5.6428 | 0.1567 | | |

**Note:** *df*, degrees of freedom; SS, sum of squares; MS, mean square.

**Fig. 4.** Otolith isotopic ratios of juvenile golden perch (*Macquaria ambigua*) reared for (*a*) 1 day and (*b*) 24 days in various combinations of enriched $^{137}Ba$ (open symbols, 0 $\mu g \cdot L^{-1}$; gray, 1 $\mu g \cdot L^{-1}$; black, 5 $\mu g \cdot L^{-1}$) and enriched $^{86}Sr$ (circles, 0 $\mu g \cdot L^{-1}$; diamonds, 25 $\mu g \cdot L^{-1}$; squares, 100 $\mu g \cdot L^{-1}$). Vertical broken line indicates natural $^{88}Sr/^{86}Sr$ ratio; horizontal broken line indicates natural $^{138}Ba/^{137}Ba$ ratio.




costly. Otolith preparation and analysis with the LA-ICP-MS cost about US$8 per otolith in this study. The cost, however, is highly dependent on labour costs and instrument fees, which can vary from one laboratory to another.

The cost of producing the mark in the otolith using stable isotopes is comparable or less expensive than other chemical marking methods. For example, 1 $g \cdot L^{-1}$ of $SrCl_2$ has been found to produce a distinct mark in the otoliths of both golden perch (Brown and Harris 1995) and sockeye salmon (Oxman et al. 2003). At this concentration (assuming the same fish densities as our experiment), the cost of marking with Sr would be about US$16 per 1000 fish. As with isotope marking, the cost of retrieving the mark is more costly than producing the mark. Preparation of otoliths would be the similar for both techniques, and either LA-ICP-MS or a scanning electron microscope with backscatter electron detector could be used to image the Sr mark (e.g., Oxman et al. 2003). Again, the cost of mark recovery would be dependent upon labour costs, instrument fees, and the time it takes to analyse the otoliths. ALC is another popular chemical mark. Typical ALC concentrations used to mark fish otoliths range from 25 to 220 $mg \cdot L^{-1}$ (Wilson 1995). Therefore, it would cost about US$24 to US$528 to mark 1000 fish with ALC. To recover the marks, a fluorescent microscope with the proper filters is required, which cost approximately US$15 000.

Marking of fish has contributed substantially to fisheries science and management in five key areas: stock contribution and use (i.e., most fisheries consist of mixed stocks and are harvested by multiple users), fish growth, fish survival, fish movement, and population estimation (Hilborn et al. 1990). For many fisheries, the majority of what is known comes from marking data (Hilborn et al. 1990). While the primary aim of this study was to develop new marking methods to identify hatchery fish and their contribution in stock enhancement projects, the potential for marking otoliths with stable isotopes goes beyond this single application.

There are several advantages of otolith marking over other techniques. Marking of otoliths using chemicals is applicable to even the youngest and smallest of life stages of all species, produces a permanent mark, can be done in batches with minimal handling of the fish, and large groups of fish can be uniquely marked (Brothers 1990). Therefore marking of otoliths could be helpful in answering different biological, ecological, and management questions. For instance, dispersal, movement, and connectivity of larval and juvenile fish populations can be studied through recapture of marked fish. Lehtonen et al. (1992) marked larval common whitefish (*Coregonus lavaretus*) with radioactive strontium ($^{85}Sr$) to measure the emigration rates from the river to the sea. Releases of marked fish in discrete locations can also be used to measure advection, diffusion, or retention around the release site (Secor and Houde 1995). The empirical data from these releases can then be used to develop and test models of larval transport, larval behaviour, and other advective–retentive forces (Secor and Houde 1995). Marked fish are also critical for developing effective stocking strategies and understanding factors affecting recruitment (e.g.,

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Bergstedt et al. 1990; Hoxmeier et al. 2006). Mark and release experiments could also provide accurate measurements of mortality and predation rates, as well as competition (Secor and Houde 1995).

Whenever working with chemicals there are always safety concerns regarding their use and disposal. The maximum concentration of Ba used (15 $\mu g \cdot L^{-1}$) is well below the drinking water guidelines for Australia, the United States, and Canada. The maximum contaminant level of Ba in drinking water for the USA is 2000 $\mu g \cdot L^{-1}$ (i.e., 2 ppm) (United States Environmental Protection Agency 2006), whereas in Canada the maximum accepted concentration is 1000 $\mu g \cdot L^{-1}$ (Health Canada – Environmental and Workplace Health 1990), and for Australia it is 700 $\mu g \cdot L^{-1}$ (National Health and Medical Research Council and Natural Resource Management Ministerial Council 2004). To our knowledge, there are no guidelines for Sr in drinking water other than for the radioactive isotopes (e.g., $^{90}Sr$). It should be stressed that the isotopes used in these experiments are naturally occurring and are stable (i.e., nonradiogenic), so the environmental health risks involved with using radioisotopes are not of concern (see Thorrold et al. 2002).

In summary, there is a need to be able to discriminate among groups of fish (e.g., stocked and wild). Currently, there are limited options for mass-marking small juvenile fish cost effectively. We have shown that enriching isotopes in rearing water of fish can produce unique isotopic marks on otoliths, with the best marks occurring after 24 days exposure to isotopes. Further testing and refinement could be done to produce more distinct marks at a number of different life-history stages (larvae, juvenile, adult). In doing this, we believe that marking fish otoliths with stable isotopes could be a viable and practical method for marking hatchery fish, which is the first step to be able to properly evaluate the success of stocking programs and measure the impacts of stocked fish on wild populations.

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# An age-structured model with leading management parameters, incorporating age-specific selectivity and maturity

**Robyn E. Forrest, Steven J.D. Martell, Michael C. Melnychuk, and Carl J. Walters**

**Abstract:** Previous authors have shown analytically that the optimal equilibrium harvest rate ($U_{MSY}$) for an iteroparous fish stock is a function of the slope of the stock–recruitment curve at low stock size ($\alpha$) and that $U_{MSY}$ can therefore be considered a direct measure of stock productivity. As such, it can be used as a leading parameter in stock assessment models and directly estimated using Bayesian or similar techniques. Here we present an alternative method for deriving $\alpha$ from $U_{MSY}$ that incorporates age-specific selectivity and fecundity, avoiding assumptions of knife-edged recruitment and maturity. We present an age-structured model with two fisheries reference points ($U_{MSY}$ and maximum sustainable yield, MSY) as its leading parameters. We show equilibrium properties of the model, chiefly in terms of its ability to show relationships between life history traits, density dependence, and $U_{MSY}$. We also demonstrate a simple Bayesian estimation routine to illustrate estimation of $U_{MSY}$ and MSY directly from data. We compare our results to those from a structurally identical model with leading biological parameters. Using models with leading management parameters can improve communicability of results to managers.

**Résumé :** Des auteurs ont montré précédemment par analyse que le taux optimal de récolte à l'équilibre ($U_{MSY}$) dans un stock de poissons itéropares est fonction de la pente de la courbe de stock–recrutement lorsque la densité du stock ($\alpha$) est faible; dans ce cas, $U_{MSY}$ peut être considéré comme une mesure directe de la productivité du stock. Cette valeur peut alors être utilisée comme variable principale dans les modèles d'évaluation des stocks et peut être estimée directement par des techniques bayésiennes ou des techniques semblables. Nous présentons ici une méthode de rechange pour dériver $\alpha$ de $U_{MSY}$ qui utilise la sélectivité en fonction de l'âge et la fécondité, évitant ainsi de faire les présuppositions associées au recrutement en lame de couteau et à la maturité. Nous présentons un modèle structuré en fonction de l'âge avec deux points de référence halieutiques ($U_{MSY}$ et le rendement soutenable maximal, MSY) comme variables principales. Nous démontrons les propriétés d'équilibre du modèle, particulièrement en ce qui a trait à sa capacité de montrer les relations entre les caractéristiques démographiques, la densité-dépendance et $U_{MSY}$. Nous faisons la démonstration d'une procédure bayésienne simple d'estimation pour évaluer $U_{MSY}$ et MSY directement à partir des données. Nous comparons nos résultats à un modèle de structure identique qui est basé sur les variables biologiques principales. L'utilisation de modèles basés sur les variables principales de la gestion peut permettre de mieux communiquer les résultats aux gestionnaires.

[Traduit par la Rédaction]

## Introduction

Maximum sustainable yield (MSY) has formed the basis of fisheries management strategies since at least the 1950s (e.g., Schaefer 1954). Despite well-documented problems with implementation of MSY policies (Larkin 1977; Punt and Smith 2001), the recent shift towards setting the fishing mortality rate that achieves MSY ($F_{MSY}$, or its dimensionless, discrete equivalent $U_{MSY}$) as a limit reference point rather than a target reference point has resulted in renewed interest in MSY as a means of determining precautionary harvest rates in both single species and ecosystem-based management contexts (Mace 2001).

Fisheries stock assessment involves estimating key parameters (leading parameters) by fitting a model to fishery-dependent or -independent data. The leading parameters of a model are those that are of greatest interest in terms of establishing reference points, even though other "nuisance" parameters (e.g., catchability, growth, and selectivity parameters) may be required for a fully specified model (Walters et al. 2006). At the very least, population models require leading parameters that determine the scale and productivity of the population, with the leading parameter describing productivity the main determinant of the behaviour of a fish stock under harvesting and, therefore, its maximum sustainable harvest rate, $U_{MSY}$. There are a number of ways that

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productivity can be represented in population models, the simplest being the logistic model's intrinsic rate of growth, $r$ (e.g., Schaefer 1954). Alternatively, some models use the slope of a stock–recruitment function near the origin, $\alpha$ (e.g., Ricker 1954; Beverton and Holt 1957). Goodyear (1977) expressed productivity in terms of the recruitment compensation ratio (CR), which is the relative improvement in juvenile survival as spawning stock abundance is reduced towards zero. In common use is a reparameterised version of the Beverton–Holt recruitment function, which uses the steepness parameter, $h$, defined as the proportion of recruits that are produced when egg production (i.e., spawner abundance) is at 20% of unfished egg production (Mace and Doonan 1988; Hilborn and Walters 1992). Myers et al. (1999) expressed $h$ (called $z$ in their paper) as a function of lifetime spawners per spawner at low abundance, $\hat{\alpha}$. Their meta-analysis, based on stock–recruitment data for more than 700 fish stocks, suggested that the magnitude of compensation in recruitment is a relatively conservative property of fish stocks, with the maximum lifetime production of spawners per spawner rarely exceeding 50. Mathematically, $\hat{\alpha}$ is the equivalent of CR under certain assumptions about fecundity (see section below). Goodwin et al. (2006) reported CR for 54 Atlantic fish stocks, again reporting CR < 50 for the majority of stocks. The finding that CR tends to be confined within certain bounds across multiple species and life histories makes CR a useful productivity parameter for modellers, especially given its analytical relationship to the more familiar $h$.

Biological productivity parameters are usually of secondary interest to managers, who tend to be more concerned with measures such as total allowable catch or maximum sustainable harvest rate. Management parameters must therefore be derived from models, using either analytical or numerical relationships. Simple surplus production models (e.g., Schaefer 1954), which do not explicitly incorporate recruitment, provide a direct analytical relationship between $r$ and $U_{MSY}$ ($U_{MSY} = r/2$). For semelparous species, $U_{MSY}$ can be expressed as a function of $\alpha$, using Ricker (1954) or Beverton and Holt (1957) recruitment functions (Hilborn and Walters 1992). Schnute and Kronlund (1996) derived analytical relationships between biological and management parameters using a generalised recruitment function for semelparous species. The resulting stock–recruitment function was parameterised in terms of two leading management parameters, $U_{MSY}$ and MSY, which could be estimated directly using established stock assessment fitting procedures. Schnute and Richards (1998) extended the approach and developed a generalised age-structured model that could be used for iteroparous species that incorporated a reparameterised stock–recruitment function in terms of $U_{MSY}$ and MSY. It assumed knife-edged selectivity and maturity and that natural and fishing mortality occurred separately. Despite these limiting assumptions, their approach enabled direct estimation of $U_{MSY}$ from data for a much broader range of species than had been previously possible.

We extend the approach of Schnute and Richards (1998) by presenting an alternative formulation of the derivation of $\alpha$ from $U_{MSY}$ that incorporates age-specific selectivity and maturity. We use an age-structured population model that utilises Botsford "incidence" functions (Botsford 1981; see Walters and Martell 2004) to calculate equilibrium eggs per recruit and vulnerable biomass per recruit, which simultaneously capture the effects of fishing and natural mortality on fish as they age. Our method avoids the assumption of knife-edged selectivity and maturity and is flexible to a wide range of selectivity and maturity schedules. These developments broaden the range of fisheries for which $U_{MSY}$ can be estimated directly.

### Links between life history and productivity

There is currently much interest in the link between life history traits and productivity, especially for species that are data-limited (Reynolds et al. 2001). Although certain life history traits (e.g., late maturity, slow growth, low natural mortality) tend to predispose species towards low values of $U_{MSY}$, density dependence in recruitment is also an important determinant. Density dependence principally refers to the improvement in juvenile survival rate as spawning stock size is reduced. Density-dependent mortality may occur at a number of life history stages but probably occurs principally in juvenile demersal stages for coastal species (Myers 2002). Mechanisms include increased territorial behaviour and greater competition for food as juvenile density increases, which lead to increased time taken to reach sizes less vulnerable to predation (see Hilborn and Walters 1992; Rose et al. 2001; Myers 2002). Foraging arena theory (Walters and Juanes 1993; Walters and Korman 1999; Walters and Martell 2004) has recently been introduced as an overarching explanation for density dependence in juvenile survival rates and predicts that density dependence is an emergent consequence of the trade-off between time spent feeding and risk of predation.

Mechanisms leading to density dependence are complex and subject to considerable interannual variability. On average, however, some species show a stronger response to changes in spawning stock size than others. All other things equal, stronger density dependence implies greater resilience to fishing due to the stock's ability to respond positively to reductions in adult biomass (e.g., Goodyear 1977). Density dependence is difficult to measure in nature because of problems with observing juvenile fish, although the meta-analyses of Myers et al. (1999) and Goodwin et al. (2006) have improved understanding of the likely range of magnitude of these effects. Quantifying interactions among life history parameters, density dependence, and sustainable harvest rates could aid in understanding the mechanisms that lead to overfishing and could be useful in design of sustainable fishing strategies. The structure of our model, with an analytical relationship between productivity and $U_{MSY}$, allows these linkages to be considered simultaneously.

### Bayesian estimation

Bayesian inference is now in mainstream use in fisheries stock assessment (e.g., Punt and Hilborn 1997; Chen et al. 2003) and has facilitated a general move towards consideration of population and management parameters as probability distributions, rather than point estimates. Once distributions of a model's leading parameters have been estimated, the past and current state of the fishery, in terms of

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population size or harvest rates, can also be estimated to determine the probability of exceeding reference points. Combining direct estimation of fishery reference points, such as MSY and $U_{MSY}$, with a Bayesian approach can improve communication of scientific results considerably (Schnute and Kronlund 1996; Schnute and Richards 1998). Managers are more familiar with the parameters MSY and $U_{MSY}$ than their more abstract biological analogues, and in fully developed fisheries, it is likely that MSY and $U_{MSY}$ lie within management experience. Dialogue between managers and scientists about the range of uncertainty to admit in stock assessments is likely to be more transparent if all parties are discussing parameters with which they are familiar.

This paper proceeds as follows. First we describe an age-structured population model that uses MSY and $U_{MSY}$ as leading parameters. Then we briefly describe some properties of the model, chiefly in terms of its ability to show relationships between life history, density dependence, and $U_{MSY}$. Finally, we implement a simple Bayesian estimation routine to illustrate estimation of $U_{MSY}$ directly.

## Population model with MSY and $U_{MSY}$ as leading parameters

The model is an age-structured population model with leading parameters MSY and $U_{MSY}$ describing scale and productivity of the population, respectively. First, we describe the equilibrium structure of the model and then incorporate time dynamics. The key difference between this model and other age-structured models is the analytical linkage between the leading management parameters and recruitment parameters.

Equilibrium recruitment ($R$) under a given constant harvest rate is a function of stock size (expressed in terms of eggs, $E$) and the leading parameters of the model. Here it is described by the Beverton and Holt (1957) recruitment function, i.e.,

$$(1) \qquad R = \frac{\alpha E}{1 + \beta E}$$

where we define a recruit as a fish of age 1. Equilibrium eggs per recruit ($\varphi_E$) can be obtained using an "incidence" function (Botsford 1981; Walters and Martell 2004), which captures the effects of natural mortality and fishing mortality over the lifetime of individuals assuming equilibrium conditions, i.e.,

$$(2) \qquad \varphi_E = \sum_a^{\infty} l_a f_a$$

where $f_a$ is relative fecundity-at-age (we assumed fecundity based on weight and a logistic maturity function; Appendix B). Survivorship-at-age, $l_a$ (the proportion of fish that survive to age $a$ under a given constant equilibrium harvest rate $U$), is given by

$$(3) \qquad l_a = \begin{cases} 1 & \text{if } a = 1 \\ l_{a-1} s_{a-1} (1 - v_{a-1} U) & \text{if } a > 1 \end{cases}$$

where $s_a$ is natural survival-at-age. We assumed $s_a$ to be constant and proportional to the von Bertalanffy growth rate, $\kappa$, via the relationship $s_a = e^{-M}$, where $M$ is the instantaneous natural mortality rate, with the simplifying assumption that $M = 1.5\kappa$ (Beverton and Holt 1959). The term $s_a(1 - v_a U)$ represents the survival rate under fishing, $s_{a\_fished}$. Equation 3 represents equilibrium survivorship under a particular constant harvesting regime and enables calculation of useful equilibrium per recruit quantities under different harvesting regimes. Note that unfished survivorship is obtained by setting $U = 0$.

At equilibrium, total egg production is given by $E = R\varphi_E$. Substituting this into eq. 1 and solving for $R$ gives

$$(4) \qquad R = \frac{\varphi_E \alpha - 1}{\beta \varphi_E}$$

Using this form of the stock–recruitment function, we show how $\alpha$ can be derived from the leading productivity parameter $U_{MSY}$ (Appendix A). The scaling parameter ($\beta$) is more easily obtained from leading parameters $U_{MSY}$ and MSY. First,

$$\mathrm{VB}_{MSY} = \frac{\mathrm{MSY}}{U_{MSY}}$$

where $\mathrm{VB}_{MSY}$ is equilibrium vulnerable biomass under $U_{MSY}$. Recruitment under $U_{MSY}$ is therefore given by

$$R_{MSY} = \frac{\mathrm{VB}_{MSY}}{\varphi_{\mathrm{VB}_{MSY}}}$$

where $\varphi_{VB}$ is vulnerable biomass per recruit at $U_{MSY}$, calculated as

$$(5) \qquad \varphi_{VB} = \sum_a^{\infty} l_a w_a v_a$$

with $l_a$ evaluated at $U = U_{MSY}$ (eq. 3) and where $w_a$ is the mean weight-at-age (derived from the von Bertalanffy (1938) growth function; see Appendix B) and $v_a$ is the mean vulnerability-at-age, defined as the proportion of fish of a given age $a$ vulnerable to the fishing gear. Asymptotic vulnerability can be represented using a simple logistic function (see Appendix B). Specification of the recruitment function can then be completed by solving eq. 4 for $\beta$ (with $R$ and $\varphi_E$ evaluated at $U_{MSY}$), i.e.,

$$\beta = \frac{\varphi_{E_{MSY}} \alpha - 1}{R_{MSY} \varphi_{E_{MSY}}}$$

Once $\alpha$ and $\beta$ are known, other important biological properties can be derived. Unfished recruitment, $R_0$, is obtained using $\varphi_{E_0}$ in eq. 4. Unfished biomass, $B_0$, is then simply a function of $R_0$ and unfished biomass per recruit, i.e., $B_0 = R_0 \varphi_{B_0}$, where

$$\varphi_{B_0} = \sum_a^{\infty} l_a w_a$$

with $l_a$ evaluated at $U = 0$.

Another productivity parameter of interest is the recruitment compensation ratio, CR (Goodyear 1977), which represents the maximum possible compensatory improvement in juvenile survival as stock size is decreased by fishing. It is easily derived from $\alpha$, i.e., unfished juvenile survival rate is

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**Table 1.** Life history and selectivity parameters used in the model.

| Parameter | Hypothetical fish | Namibian Cape hake |
|---|---|---|
| $L_\infty$ | 60 cm | 111 cm[a] |
| $\kappa$ | 0.12·year$^{-1}$ | 0.14·year$^{-1}$ [a] |
| $a_0$ | –0.5 | 0 |
| *lwa* | 0.0001 | 0.00001[b] |
| *lwb* | 3 | 3[b] |
| $a_{max}$ | 15 years | 25 years[b] |
| $a_{mat}$ | 2 years | 4 years[c] |
| $a_0$ | 3 years | 3 years[d] |

**Note:** $L_\infty$, theoretical maximum length of the fish; $\kappa$, instantaneous growth rate; $a_0$, theoretical age at which the fish has zero length; $a_{mat}$, age at 50% maturity; $a_{max}$, maximum age; $a_0$, age at 50% first harvest. Length is converted to weight using the conversion factors *lwa* and *lwb*, i.e., $w_a = lwa \cdot L_a^{lwb}$, where $L_a$ is the length at age $a$.

[a]Jones 1974 (cited in FishBase, www.fishbase.org).

[b]These parameters produced the approximate mean maximum weight cited in FishBase (www.fishbase.org).

[c]Hilborn and Mangel 1997.

[d]Arbitrarily assigned.

$R_0/E_0$, but, $\varphi_{E_0} = E_0/R_0$, so unfished survival is simply $\varphi_{E_0}^{-1}$. As juvenile survival at very low stock size is $\alpha$, CR is just the ratio of these two survival rates (Goodyear 1977), i.e.,

$$\text{(6)} \qquad \text{CR} = \alpha\varphi_{E_0}$$

When relative fecundity is described as the product of mean weight-at-age and maturity-at-age (Appendix B), $\varphi_{E_0}$ is the same as unfished spawning biomass per recruit ($\text{SPR}_{F=0}$; Gabriel et al. 1989). Myers et al. (1999) defined maximum lifetime spawners per spawner ($\hat{\alpha}$) as the product of $\alpha$ and $\text{SPR}_{F=0}$ and, therefore, the same as CR. When Beverton–Holt recruitment is assumed, the steepness parameter, $h$, of Mace and Doonan (1988) is related to $\hat{\alpha}$ (i.e., CR) by $h = \hat{\alpha}/(4 + \hat{\alpha})$ (Myers et al. 1999).

The model is made dynamic by simulating changes in numbers $N$ at age $a$ and years $t$ via the equation

$$\text{(7)} \qquad N_{a+1,t+1} = N_{a,t}s_a(1 - v_{a,t}U_t) \quad \text{(for } a > 1 \text{ and } t > 1\text{)}$$

Annual harvest rate, $U_t$, is calculated from annual catch, $C_t$:

$$\text{(8)} \qquad U_t = \frac{C_t}{\text{VB}_t}$$

where $\text{VB}_t$ is the biomass of fish vulnerable to the fishing gear,

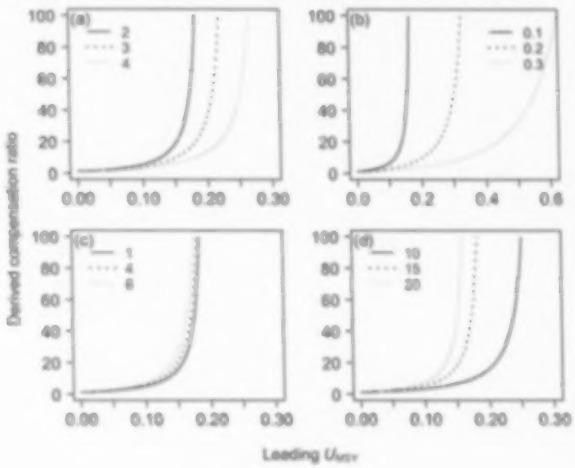
$$\text{(9)} \qquad \text{VB}_t = \sum_a N_{a,t}v_{a,t}w_a$$

Recruits ($R_t$, i.e., $N_{1,t}$) are added to the population using eq. 1 with number of eggs calculated as

$$E_t = \sum_a^{\infty} f_a N_{a,t}$$

We made the common simplifying assumption that the unfished stock was at equilibrium and initialised the model in the first year of fishing with $N_{a,1} = R_0 I_a$.

**Fig. 1.** Effect of different values of (*a*) age at 50% first harvest, $a_0$ (years); (*b*) von Bertalanffy growth rate, $\kappa$ (year$^{-1}$); (*c*) age at 50% maturity, $a_{mat}$ (years); and (*d*) maximum age, $a_{max}$ (years) on the relationship between leading productivity parameter $U_{MSY}$ and the derived compensation ratio (CR) for a hypothetical species. Parameter values are provided in Table 1. Note truncation of the *y* axis at CR = 100 and different scales on the *x* axes.




## Equilibrium properties: relationships between life history, density dependence, and $U_{MSY}$

The equilibrium model can be used to examine the predicted form of the relationship between density dependence (measured by CR) and $U_{MSY}$. The effect of gear selectivity and life history traits (e.g., growth rate, age-at-maturity, maximum age, and natural mortality) on this relationship can also be modelled. Here, we consider a hypothetical fish species with known life history parameters (Table 1) and show the effect of increasing (*i*) age at first harvest, (*ii*) von Bertalanffy growth rate, (*iii*) age-at-maturity, and (*iv*) maximum age on the relationship between CR and $U_{MSY}$. To do this, $\alpha$ was calculated over a range of hypothesised values of $U_{MSY}$ (0 to 1, step size 0.0001) using eq. A6 and converted to CR (eq. 6).

We show the form of the relationship between CR and $U_{MSY}$ (note that $U_{MSY}$ is the independent variable; Fig. 1). The relationship is not dynamic but rather shows the predicted values of CR under a range of hypothesised values of $U_{MSY}$ (i.e., the degree of improvement in juvenile survival that would be required for each hypothesised value of $U_{MSY}$ to be true). As the hypothesised value of $U_{MSY}$ increases, the strength of recruitment compensation that would be needed for the hypothesis to be true increases rapidly and tends towards a vertical asymptote. Values of $U_{MSY}$ to the right of the asymptote are undefined, representing hypotheses of $U_{MSY}$ for which $\alpha$ was predicted to be negative (therefore impossible). We have truncated the *y* axis in Fig. 1 at CR = 100 because as $U_{MSY}$ approached its maximum possible value, CR tended rapidly towards very large values, making comparison of the curves difficult. Because most of the

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curves become almost vertical by the truncation point, the maximum possible value of $U_{MSY}$ can still be seen. As values of CR > 100 seem to be rare (Myers et al. 1999; Goodwin et al. 2006), the region of management interest is shown (Fig. 1).

The relationship between CR and $U_{MSY}$ at different values of age at 50% first harvest, $a_h$, is shown (Fig. 1*a*). Increasing $a_h$ causes the curve to shift to the right, increasing the range of values of $U_{MSY}$ that can be considered possible. Increasing $\kappa$ (von Bertalanffy growth rate and proxy for natural mortality) causes the curve to shift to the right, implying a greater range of possible values of $U_{MSY}$ for faster-growing species (Fig. 1*b*). Increasing age at 50% maturity, $a_{mat}$ (Fig. 1*c*), or maximum age, $a_{max}$ (Fig. 1*d*), however, causes the curve to shift to the left, implying a smaller range and lower possible values of $U_{MSY}$ for later-maturing or longer-lived species (although the effect of age-at-maturity is small). Importantly, Figure 1 suggests that, for some species for which Beverton–Holt recruitment can be assumed, there is a maximum possible value of $U_{MSY}$ that can be estimated from life history and selectivity data alone.

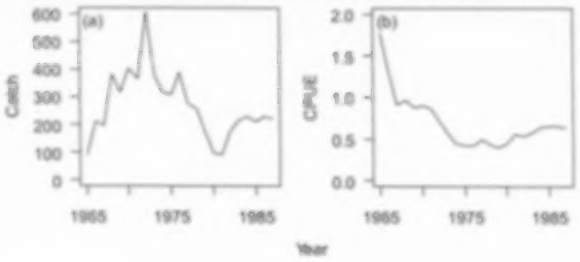
## Bayesian estimation of MSY and $U_{MSY}$

### Methods

In this section, we use our model to show how MSY and $U_{MSY}$ and can be estimated using a Bayesian approach. We used catch and catch per unit effort (CPUE) data (Fig. 2) for Namibian Cape hake (a mixed stock of *Merluccius capensis* and *Merluccius paradoxus*) published in Hilborn and Mangel (1997). We chose this data set because (*i*) it will be familiar to many readers and (*ii*) CPUE is considered to be a reasonable index of abundance because the degree of schooling in hake is relatively low. The fishery began in the mid-1960s and was largely unregulated, resulting in a large decline in CPUE in the first 10 years. Following conservation concerns, catches were reduced in the 1970s, which resulted in a slight increase in CPUE (Hilborn and Mangel 1997). Life history and selectivity parameters are provided in Table 1.

We compare our model with leading management parameters (MSY and $U_{MSY}$; model 1) with one with leading biological parameters ($R_0$ and CR; model 2) to show that very similar results can be obtained using either approach. Model 2 was identical in structure to model 1, except for the method of calculating the parameters of the recruitment function (i.e., in model 2, $\alpha$ was obtained from the leading value of CR and eq. 6; $\beta$ was then obtained from the leading value of $R_0$ and eq. 4). In both models, in addition to estimating the leading parameters, we also estimated the instantaneous natural mortality rate, $M$, and the standard deviation of the observation error anomalies, $\sigma$. To obtain the posterior distributions, we used a Metropolis–Hastings algorithm implemented in R, using the function "MCMCmetrop1R" in the MCMC package (Martin and Quinn 2006; R Development Core Team 2006). Markov chain simulation performs a random walk in the parameter space of $\theta$ (model 1, $\theta$ = (MSY, $U_{MSY}$, $M$, $\sigma$); model 2, $\theta = (R_0, CR, M, \sigma)$), which converges to a distribution that approximates the joint posterior distribution (Gelman et al. 1995). The algorithm was initialised at the maximum likelihood estimates for $\theta$ and proceeded for 110 000 iterations, the first 10 000 of which were discarded to allow for convergence. Convergence was assessed by visually examining trace plots and plotting running medians of length 50 to ensure that the algorithm was sampling from a stable distribution (see Gelman et al. (1995) and Punt and Hilborn (1997) for more details on MCMC methods).

**Fig. 2.** (*a*) Catch (thousands of tons) and (*b*) catch per unit effort (CPUE; tons per standardised trawler hour) used to fit the models for Namibian Cape hake. Data source: Hilborn and Mangel (1997).




For simplicity we did not try to estimate process error. We assumed lognormal observation error, i.e., $CPUE_t = qVB_t e^{\varepsilon_t}$, where $q$ is the constant of proportionality (catchability) and $\varepsilon_t \sim N(0, \sigma)$. We treated $\sigma$ and $q$ as uncertain parameters but used the maximum likelihood estimate (MLE) of $q$ in the joint posterior distribution, using the approach of Walters and Ludwig (1994), i.e., assuming a linear relationship between $CPUE_t$ and $VB_t$, we estimated $z_t = \ln(CPUE_t) - \ln(VB_t)$ and

$$\bar{z} = \frac{\sum_t z_t}{n} \tag{10}$$

The MLE of $q$ was then $e^{\bar{z}}$ and the observation residuals ($d_t$) used in the log-likelihood function were calculated as $d_t = z_t - \bar{z}$. The log-likelihood of each observation was thus

$$L_t = \ln(\sigma) + 0.5\ln(2\pi) + \frac{d_t^2}{2\sigma_t^2} \tag{11}$$

We assumed uninformative prior probability distributions for $U_{MSY}$ and MSY in model 1 and for $R_0$ in model 2. We assumed a normally distributed prior for $M$, i.e., $M \sim N(0.21, 0.1)$, with the mean based on the assumption $M = 1.5\kappa$ (Beverton and Holt 1959). We assumed a weak, lognormally distributed informative prior for CR to penalise negative (i.e., impossible) values of CR. We log-transformed $R_0$, CR, and MSY so that the relative scales of parameters in the search routine were similar. $U_{MSY}$ was logit-transformed to constrain values between 0 and 1.

MSY and $U_{MSY}$ had to be estimated numerically in model 2. For each $\theta$, we used a Newton–Raphson algorithm to search over the derivative of the yield function (eq. A1) with respect to $U$ to find the value of $U$ that maximised yield. Note that we may not have used the most current parameters for these hake species and have likely used an incorrect selectivity schedule. Our choice of priors for CR and $M$ will also influence our results, which should therefore be read as illustrative only.

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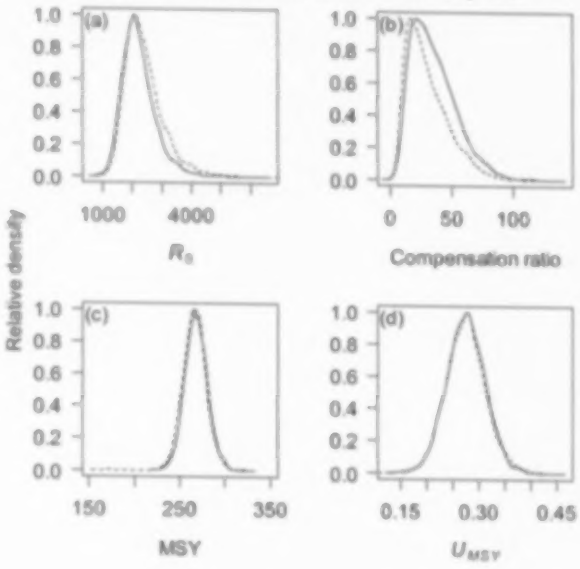
## Results

The weak prior placed on CR had the effect of constraining the posterior values of $U_{MSY}$ and MSY to values that were not associated with impossible recruitment parameters (see life history section). The prior placed on $M$ constrained this parameter within plausible biological bounds (i.e., close to 1.5κ; Beverton and Holt 1959) and therefore also prevented $U_{MSY}$ from becoming large. Our choice of $a_b$ relative to $a_{mat}$ also affected the results. For fish populations in which most individuals vulnerable to the fishing gear have already had the opportunity to spawn, $U_{MSY}$ must approach unity. Alternatively, harvesting a population at an age before most individuals have spawned results in lower sustainable harvest rates (this is implicit in Fig. 1*a*).

Estimation of key management parameters was robust to the choice of leading parameters (Fig. 3). Density plots of the posterior distributions of the leading parameters in each model are shown (Fig. 3). The two models give very similar results for the biological parameters and almost identical results for the management parameters. Note that $R_0$ and CR were obtained analytically in model 1 and that MSY and $U_{MSY}$ were estimated numerically in model 2. There was no evidence that the parameter estimates did not converge (Fig. 4).

**Fig. 3.** Density plots showing relative posterior probability density distributions of $R_0$, compensation ratio (CR), maximum sustainable yield (MSY), and $U_{MSY}$ for model 1 (broken line) and model 2 (solid line). Plots obtained from Markov chain Monte Carlo (MCMC) sample of length 100 000 (burn-in: 10 000 cycles).




## Discussion

Schnute and Kronlund (1996) derived α from $U_{MSY}$ for semelparous species. They demonstrated the advantages of their reparameterised recruitment function in terms of its amenability to Bayesian fitting procedures and, because a parameter with policy relevance could be directly estimated from data, improved communicability of results. The idea was extended to a generalised age-structured model for iteroparous species by Schnute and Richards (1998), who assumed knife-edged maturity and recruitment. The approach presented here extends these previous works by allowing the inclusion of age-specific maturity and recruitment via the Botsford "incidence" functions, which incorporate age schedules of fecundity, mortality, and vulnerability. We demonstrated the approach using logistic, age-based selectivity and maturity schedules, but the approach is flexible to any formulation of these. For example, dome-shaped or lognormal selectivity curves may be more appropriate for species in which large or old individuals are able to escape fishing because of behavioural, spatial, or market-based effects. We made certain simplifying assumptions, notably that $M = 1.5\kappa$. This relationship, suggested by Beverton and Holt (1959) to be an invariant property of fish populations, is widely applied in fisheries models. However, our model is flexible to this assumption, as well as to the assumption that $M$ is constant with age.

We used our model to illustrate some important relationships between density dependence, life history traits, and $U_{MSY}$. We stress that the relationship between CR and $U_{MSY}$ shown in Fig. 1 is not dynamic, but rather represents the degree of improvement in juvenile survival that would be required for each hypothesised value of $U_{MSY}$ to be true. For a species with a given growth, survival, maturity, and selectivity schedule, there will be a mean curve describing the relationship between $U_{MSY}$ and CR representing the set of values of CR and $U_{MSY}$ that can be considered possible for the species. This curve can be calculated from life history and selectivity parameters alone, prior to any time series fitting. Figure 1 implies that for some species, there will be a finite range of possible values of $U_{MSY}$, with its upper bound at the asymptotic value of $U_{MSY}$. This is because $U_{MSY}$ maximises yield in terms of weight and is therefore determined by growth, survival, and selectivity (Beverton and Holt 1957). The upper bound of $U_{MSY}$ represents the harvest rate beyond which long-term yield can no longer be maximised for a given growth and selectivity schedule, no matter how strong recruitment compensation is. If there is no other prior information about the productivity of a species and Beverton–Holt type recruitment can be assumed, then there is an upper boundary of $U_{MSY}$ that can be estimated from life history and selectivity data alone. For species with very steep $U_{MSY}$–CR curves (curves with an upper boundary very far to the left of the $U_{MSY}$ axis), uncertainty in $U_{MSY}$ can be reduced considerably, even if the actual value of $U_{MSY}$ cannot be estimated because of a lack of historical data. If reasonable estimates of CR are available for similar species or from meta-analysis, it may also be possible to construct a reasonable prior for $U_{MSY}$ for data-limited species.

The effects of selectivity and life history parameters on the relationship between CR and $U_{MSY}$ are not surprising. Increasing (long-term) age at 50% first harvest, $a_b$, causes the $U_{MSY}$–CR curve to become less steep and shift to the right. Assuming that the value of CR is a fixed property of a population independent of $a_b$, this implies that a greater maximum sustainable harvest rate could be achieved by more selective fishing gear allowing younger fish to escape. This idea is a well-known result of per-recruit type analyses (Beverton and Holt 1957). The relationship between κ and

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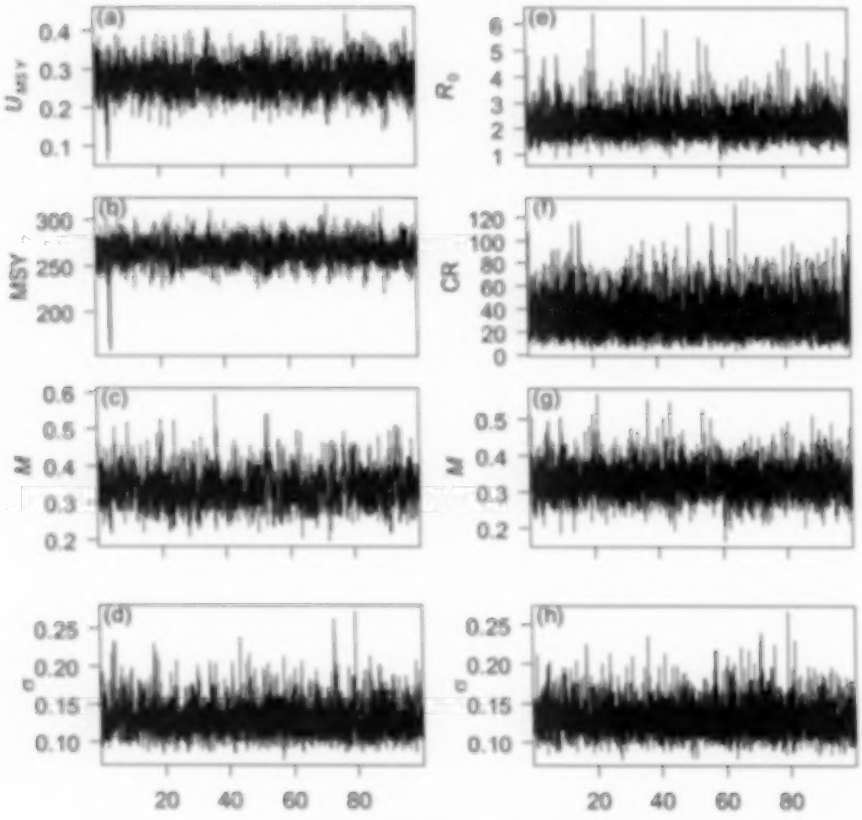
**Fig. 4.** Trace plots of iterations versus sampled values for each estimated parameter indicating convergence of the estimates. Results are shown for model 1: (*a*) $U_{MSY}$, (*b*) maximum sustainable yield (MSY), (*c*) $M$, and (*d*) $\sigma$; and model 2: (*e*) $R_0$ (thousands), (*f*) compensation ratio (CR), (*g*) $M$, and (*h*) $\sigma$.




$U_{MSY}$ was also very strong. In our equilibrium formulation, $\kappa$ was used in the model twice: (*i*) as growth rate affecting the rate at which fish reach maximum weight and (*ii*) as a proxy for natural mortality, $M$, affecting the survivorship schedule (eq. 3). Although these two effects are confounded, they have the same qualitative effect on the $U_{MSY}$–CR curve, i.e., increasing $\kappa$ caused the curve to become less steep. For a given value of $U_{MSY}$, the amount of recruitment compensation required to support that $U_{MSY}$ is less for faster-growing species because (*i*) asymptotic maximum weight is reached earlier and (*ii*) the population has faster turnover. Increasing $a_{max}$ had a weak influence on the relationship between $\kappa$ and $U_{MSY}$, although it did cause a slight increase in steepness and a shift to the left. All other things equal, species with later maturity have a smaller lifetime reproductive capacity and a greater chance of being harvested before they have reproduced. Increasing $a_{max}$ similarly caused the curve to shift to the left. Higher CR required to support a given $U_{MSY}$ for longer-lived species could be a result of the relatively smaller contribution of older age classes to the total yield due to the decaying survivorship function.

It should be noted that life history parameters tend to covary and can rarely be considered in isolation, i.e., longer-lived species tend to mature later, grow slower, and have lower natural mortality. We chose to separate out the effects of single parameters on the steepness of the $U_{MSY}$–CR curve, not because these curves have applicability in themselves, but because they allow the complexity of the interaction between life history traits, selectivity, density dependence, and sustainable harvest rate to be seen. Maximum sustainable harvest rate is not a simple function of selectivity, density dependence, or individual life history parameters but a complex result of them all. Simplistic assumptions about the effects of one of these factors on $U_{MSY}$ should not be made without consideration of the other influential factors.

Life history information is easier and cheaper to obtain than recruitment and abundance data and is routinely collected. Growing conservation concerns and current trends towards more ecosystem-based approaches of managing fisheries (e.g., Food and Agriculture Organization of the United Nations 2003; Pikitch et al. 2004) require consideration of the impacts of fisheries on many more species than previously and there is now a very large body of literature studying the link between life history traits and productivity for data-limited fish. For example, McAllister et al. (2001) demonstrated three approaches that could be used to esti-

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mate $r$ for elasmobranchs using only life history information. Beddington and Kirkwood (2005) presented a method for estimating $F_{MSY}$ based on Beverton and Holt (1959) invariants and parameters describing growth, length at first capture, and the steepness parameter, $h$. Goodwin et al. (2006) showed correlations between a composite life history parameter (unfished spawners per recruit, $SPR_{F=0}$), Ricker $\alpha$, and CR for 54 Atlantic teleosts for which stock–recruitment data were available. They found a strong negative correlation between $SPR_{F=0}$ and $\alpha$ and a positive correlation between $SPR_{F=0}$ and CR and discussed evolutionary reasons for these observations. Jennings et al. (1999) and Denney et al. (2002) also searched for correlations between life history and productivity. The general approach of these papers was to analyze stocks for which informative data exist about productivity (e.g., measured as population response to fishing pressure) and draw conclusions that could be used in development of management strategies for data-limited species. We suggest that our model could contribute to such approaches as it provides a link between life history, density dependence, and $U_{MSY}$ simultaneously.

We used a simple Bayesian estimation routine to illustrate the parameter estimation process. We compared a model with leading management parameters (MSY and $U_{MSY}$) with a model structurally identical except for its leading parameters ($R_0$ and CR). We showed that the same posterior probability densities for management parameters could be obtained in either case. However, we argue that the first model is advantageous for two reasons: (*i*) it is more efficient (there is no need to numerically estimate MSY and $U_{MSY}$) and (*ii*) it enables improved communication of scientific results. Determination of appropriate informative priors is one of the most difficult aspects of stock assessment (see Punt and Hilborn 1997), and the preliminary phases of stock assessment often involve intensive modelling and testing sessions to determine plausible ranges of leading biological parameters. These ranges are often based on the plausibility of the model's predicted MSY (or $U_{MSY}$). Hoenig et al. (1994) have suggested methods for constructing informative priors on MSY based on historical catch and effort data. Simple analytical relationships have also been suggested for obtaining rough estimates of MSY and $U_{MSY}$ (e.g., Gulland 1971; Patterson 1992), which could be used in construction of priors. Models such as ours and that of Schnute and Richards (1998) enable this information to be used in direct estimation of $U_{MSY}$, a parameter of primary management interest. We suggest that dialogue between scientists and managers will be improved if the parameters at the forefront of the analysis are familiar to all parties. We suggest this may work in both directions, as managers with a long history of involvement in a fishery will be better able to contribute to the stock assessment process if the focus is on parameters with which they have direct experience.

In summary, we have presented a model that has several advantages: (*i*) it enables direct estimation of parameters of principle management interest; (*ii*) it is flexible to a very wide range of assumptions about growth, survival, maturity, and selectivity, including the form of these relationships; and (*iii*) it provides a means of analysing the interaction among important selectivity and life history parameters, density dependence, and maximum sustainable harvest rate. It is amenable to Monte Carlo type approaches to account for uncertainty in input parameters, as well as to Bayesian or likelihood approaches for estimating leading parameters.

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## Appendix A. Derivation of $\alpha$ from $U_{MSY}$

For a given selectivity schedule, equilibrium yield ($Y$) for any long-term fixed exploitation rate ($U$) is predicted to be

$$\text{(A1)}\quad Y = UR\varphi_{VB}$$

where recruits ($R$) are defined as fish of age 1 and $\varphi_{VB}$ is equilibrium vulnerable biomass per recruit (eq. 5). Substituting the Beverton–Holt recruitment function (eq. 4) into eq. A1 and rearranging gives

$$\text{(A2)}\quad Y = \frac{\alpha U\varphi_{VB}}{\beta} - \frac{U\varphi_{VB}}{\beta\varphi_E}$$

There are actually three functions of $U$ contained in eq. A2 because $l_a$ (a component of the functions $\varphi_{VB}$ and $\varphi_E$) is also a function of $U$. $Y$ is a convex function of $U$, with $Y = 0$ at either $U = 0$ or $U_{extinction}$ and maximum $Y$ occurring between these at $U_{MSY}$. Solving

$$\frac{\partial Y}{\partial U} = 0$$

for $U$ therefore gives the value of $U$ that maximises the function (i.e., $U_{MSY}$). Differentiating $Y$ with respect to $U$ in eq. A2 gives

$$\text{(A3)}\quad \frac{\partial Y}{\partial U} = \frac{\alpha\varphi_{VB}}{\beta} + \frac{\alpha U}{\beta}\left(\frac{\partial\varphi_{VB}}{\partial U}\right) - \frac{\varphi_{VB}\varphi_E + U\varphi_E\left(\frac{\partial\varphi_{VB}}{\partial U}\right) - U\varphi_{VB}\left(\frac{\partial\varphi_E}{\partial U}\right)}{\beta\varphi_E^2}$$

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Setting $\frac{\partial Y}{\partial U} = 0$ and solving for $U_{MSY}$ gives

$$(A4)\quad U_{MSY} = \frac{1 - \alpha\varphi_E}{\frac{\alpha\varphi_E - 1}{\varphi_{VB}}\left(\frac{\partial\varphi_{VB}}{\partial U_{MSY}}\right) + \frac{1}{\varphi_E}\left(\frac{\partial\varphi_E}{\partial U_{MSY}}\right)}$$

with $\varphi_E$ and $\varphi_{VB}$ evaluated at $U_{MSY}$. Note that the stock–recruitment scalar $\beta$ is absent from eq. A4, as $U_{MSY}$ is independent of the units used to count the population.

By setting

$$k_1 = \left(\frac{\partial\varphi_E}{\partial U_{MSY}}\right)\varphi_E^{-1} \text{ and } k_2 = \left(\frac{\partial\varphi_{VB}}{\partial U_{MSY}}\right)\varphi_{VB}^{-1}$$

eq. A4 can be expressed as

$$(A5)\quad U_{MSY} = \frac{1 - \alpha\varphi_E}{k_1 + k_2(\alpha\varphi_E - 1)}$$

and

$$(A6)\quad \alpha = \frac{1 - k_1 U_{MSY} + k_2 U_{MSY}}{\varphi_E(1 + k_2 U_{MSY})}$$

$\frac{\partial\varphi_E}{\partial U_{MSY}}$ and $\frac{\partial\varphi_{VB}}{\partial U_{MSY}}$ can be solved analytically as recursive functions of $\varphi_E$ and $\varphi_{VB}$ in the following manner. Equation 5 expressed $\varphi_{VB}$ as the sum of the product of survivorship-to-age ($l_a$), vulnerability-at-age ($v_a$), and weight-at-age ($w_a$). Expanding eq. 5 gives

$$(A7)\quad \frac{\partial\varphi_{VB}}{\partial U_{MSY}} = \frac{\partial l_1 v_1 w_1}{\partial U_{MSY}} + \frac{\partial l_2 v_2 w_2}{\partial U_{MSY}} + \frac{\partial l_3 v_3 w_3}{\partial U_{MSY}} + \ldots + \frac{\partial l_\infty v_\infty w_\infty}{\partial U_{MSY}}$$

Assuming that mean weight-at-age is independent of harvest rate, then the $v$ and $w$ terms factor out of the derivatives. Because $l_1$ (survivorship at age 1) is, by definition, 1, its derivative with respect to $U_{MSY}$ is zero, so the first term disappears. Therefore,

$$(A8)\quad \frac{\partial\varphi_{VB}}{\partial U_{MSY}} = \sum_a^\infty v_a w_a \frac{\partial l_a}{\partial U_{MSY}}$$

$\frac{\partial l_a}{\partial U_{MSY}}$ is then easily obtained, i.e., $l_a = l_{a-1}s_{a-1\_fished}$, where $s_{a-1\_fished}$ is given by $s_{a-1}(1 - v_{a-1}U)$ with $U$ set to $U_{MSY}$. The derivative of $s_{a-1\_fished}$ with respect to $U_{MSY}$ is simply $(-s_{a-1}v_{a-1})$ and, therefore,

$$(A9)\quad \frac{\partial l_a}{\partial U_{MSY}} = s_{a-1}(1 - v_{a-1}U_{MSY})\left(\frac{\partial l_{a-1}}{\partial U_{MSY}}\right) - l_{a-1}s_{a-1}v_{a-1}$$

Because $\frac{\partial l_a}{\partial U_{MSY}}$ is by definition zero, eq. A9 can be solved recursively and substituted into eq. A8. $\frac{\partial\varphi_E}{\partial U_{MSY}}$ is solved in exactly the same way, except that $f_a$ is used instead of $v_a w_a$. The parameters $k_1$ and $k_2$ can now be solved and substituted into eq. A6 to give a function expressing $\alpha$ in terms of a leading productivity parameter, $U_{MSY}$. The resulting formula can be easily implemented in a spreadsheet or any appropriate programming language. The derivation can be checked numerically by running the model under a range of constant harvest rates and checking that the harvest rate that produces maximum long-term yield is the same as the leading $U_{MSY}$.

Note that, if desired, eqs. 3 and A9 can easily be modified to include a plus group (i.e., individuals of age $a_{max}$ and older). For $a = a_{max}$, survivorship would be given by

$$l_a = \frac{l_{a-1}s_{a-1\_fished}}{1 - s_{a-1\_fished}}$$

For $a = a_{max}$, $\frac{\partial l_a}{\partial U_{MSY}}$ would then be given by

$$(A10)\quad \frac{\partial l_a}{\partial U_{MSY}} = \frac{(1 - s_{a\_fished})\left(s_{a-1}(1 - v_{a-1}U_{MSY})\left(\frac{\partial l_{a-1}}{\partial U_{MSY}}\right) - l_{a-1}s_{a-1}v_{a-1}\right) - s_a v_a s_{a-1\_fished} l_{a-1}}{(1 - s_{a\_fished})^2}$$

## Appendix B. Growth, maturity, and gear selectivity functions

### Growth schedule

We assumed von Bertalanffy (1938) growth:

$$(B1)\quad L_a = L_\infty(1 - e^{-\kappa(a - a_0)})$$

where $L_a$ is the length at age $a$, $L_\infty$ is the theoretical maximum length of the fish, $\kappa$ is the instantaneous growth rate, and $a_0$ is the theoretical age at which the fish has zero length. Length is converted to weight using the conversion factors $lwa$ and $lwb$, i.e., $w_a = lwa \cdot L_a^{lwb}$

### Maturity and selectivity schedules

We assumed logistic gear selectivity and maturity schedules, as we believe these to be common in fisheries, although other appropriate formulations could be substituted for these.

Relative fecundity-at-age, $f_a$, was assumed proportional to body weight and was modelled as

$$(B2)\quad f_a = w_a \mathrm{Mat}_a$$

where maturity-at-age ($\mathrm{Mat}_a$) is given by the following logistic function:

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$$\text{(B3)}\quad \text{Mat}_a = \frac{1}{1 + e^{\left(\frac{-(a - a_{50,1})}{\sigma}\right)}}$$

where $\sigma$ determines the steepness of the curve, with smaller values of $\sigma$ resulting in a steeper curve. We assumed $\sigma = 0.2a_{max}$, implying a relatively steep curve (i.e., most individuals mature around the same age).

Similarly, vulnerability to fishing gear at age ($v_a$) is given by

$$\text{(B4)}\quad v_a = \frac{1}{1 + e^{\left(\frac{-(a - a_{v,1})}{\sigma}\right)}}$$

with $\sigma = 0.1a_k$. This implies a relatively steep selectivity schedule. In the absence of other information, it is fairly common to assume steep or knife-edged maturity and selectivity schedules.

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# The influence of air temperature, groundwater discharge, and climate change on the thermal diversity of stream fishes in southern Ontario watersheds

**Cindy Chu, Nicholas E. Jones, Nicholas E. Mandrak, Andrew R. Piggott, and Charles K. Minns**

**Abstract:** The availability of suitable thermal habitat for fishes in streams is influenced by several factors, including flow, channel morphology, riparian vegetation, and land use. This study examined the influence of air temperature and groundwater discharge, predictors of stream temperature, on the thermal diversity (cold-, cool-, and warm-water preferences) of stream fish communities in southern Ontario watersheds. Site-level fish sampling data were used to assess the thermal diversity of 43 quaternary watersheds using three metrics, the proportion of sites within a watershed having (*i*) cold-, (*ii*) cool-, and (*iii*) warm-water fishes. Our results indicated that 53.9% of the variances in cold-water and 54.1% of the variances in warm-water fish distributions within the watersheds could be attributed to groundwater discharge and air temperature variables. Climate change scenarios suggested that watersheds with high groundwater discharge and the associated thermal diversity of fishes within those watersheds are less sensitive to climate change than watersheds with low groundwater discharge. Conservation of groundwater resources will be required to lessen climate change impacts on the thermal habitat and thermal diversity of stream fishes in southern Ontario watersheds.

**Résumé :** La disponibilité d'habitats adéquats au niveau thermique pour les poissons dans les cours d'eau est influencée par de nombreux facteurs, dont le débit, la morphologie du chenal, la végétation de la rive et l'utilisation des terres. Notre étude examine l'influence de la température de l'air et de l'apport d'eau souterraine, des variables explicatives de la température des cours d'eau, sur la diversité thermique (préférences pour les eaux froides, fraîches ou chaudes) des peuplements de poissons d'eau courante dans des bassins versants du sud de l'Ontario. Des données d'inventaire des poissons à l'échelle du site ont servi à évaluer la diversité thermique de 43 bassins versants quaternaires à l'aide de trois métriques, soit les proportions des sites dans le bassin versant qui ont des poissons (*i*) d'eau froide, (*ii*) d'eau fraîche et (*iii*) d'eau chaude. Nos résultats indiquent que 53,9 % des variances des répartitions des poissons d'eau froide et 54,1 % des variances des répartitions des poissons d'eau chaude dans les bassins versants peuvent s'expliquer par les variables d'écoulement d'eau souterraine et de température de l'air. Des scénarios de changement climatique indiquent que les bassins versants ayant de forts écoulements d'eau souterraine et une diversité thermique correspondante de poissons sont moins sensibles au changement climatique que les bassins versants à faible écoulement d'eau souterraine. Il sera nécessaire d'assurer la conservation des ressources d'eau souterraine si l'on veut diminuer les impacts du changement climatique sur les habitats thermiques et la diversité thermique des poissons d'eau courante dans les bassins versants du sud de l'Ontario.

[Traduit par la Rédaction]

## Introduction

Climate change is expected to increase in-stream temperatures (in this paper, streams refers to all watercourses from headwater streams to large rivers), alter the timing of the spring freshet, and disrupt annual stream flow patterns (McCarthy et al. 2001; Mohseni et al. 2003). These effects may lead to a reduction in fish species richness (Xenopoulos et al. 2005) and suitable fish habitat (Meisner 1990). Climate change may also facilitate the expansion of invasive or pred-

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atory species that could negatively impact native fishes (Jackson and Mandrak 2002). The increased demands for fresh water and freshwater resources will strain the quantity and quality of water flowing through streams in Canada (Schindler 2001). The successful management and maintenance of ecological integrity in streams will depend on our ability to assess, adapt, and mitigate future climate change impacts.

In streams, water temperature and, consequently, thermal habitat are influenced by air temperature, precipitation, relative humidity, flow, geology, topography, land use, watershed vegetation, channel and floodplain morphology, and riparian vegetation (Poole and Berman 2001). However, air temperature has been identified as a main predictor of stream temperatures (Poole and Berman 2001), and groundwater discharges into streams have been identified as crucial components of suitable thermal habitat for fishes (Power et al. 1999).

Seasonal changes in air temperatures cause concurrent changes in stream temperatures. Stoneman and Jones (1996) found that sites within southern Ontario streams may be designated as cold, cool, or warm water from the relationship between maximum daily air temperatures and daily water temperatures at 1600 hours (maximum temperatures) in the summer. Groundwater discharge to a stream provides a constant influx of water at a temperature that approximates the mean annual air temperature (8 °C in southern Ontario; Power et al. 1999; Meteorological Service of Canada 2004). Consequently, groundwater discharge provides thermal refugia for species that prefer cooler temperatures in the summer while providing habitat free of ice for all species in the winter. Fishes actively seek and inhabit these refugia in both summer and winter (Power et al. 1999). The interaction between air and groundwater temperatures provides thermally diverse habitats in streams that should support a diversity of thermal guilds and influence the distribution of those thermal guilds within a watershed.

Given the potential impacts of climate change on streams and the influence of air temperature and groundwater discharge on the thermal habitat of stream fishes, the objectives of our study were to assess the current thermal diversity of stream fish communities in Ontario, determine how air temperature and groundwater influence those diversities, and predict the potential impacts of climate change on thermal diversity.

## Materials and methods

### Study area

Southern Ontario (Fig. 1) supports the greatest biodiversity of freshwater fishes in Canada, with 106 out of a total 229 species occurring in several of the tertiary watersheds (Chu et al. 2003). This rich biodiversity can be attributed to postglacial dispersal, human activities, and climate. The proximity of southern Ontario to the Mississippian refugium facilitated the dispersal of 72 fishes into southern Ontario after the Wisconsinan ice age (Mandrak and Crossman 1992). Human activities have led to the introductions of several fishes via ballast water, stocking, canals, boats, and aquaculture (Dextrase and Mandrak 2006). The cold winters (mean of –6 °C) and mild summers (mean of 20 °C) (Meteorological Service of Canada 2004) support cool-water fishes, the lower distributional limits of cold-water fishes, and the upper distributional limits of warm-water fishes (Shuter et al. 2002).

### Data layers

Quaternary watershed boundaries, stream network, fish community information, air temperature, and groundwater data were required to conduct the analyses needed to meet the objectives of this study. Climate change scenarios simulating future air temperatures were also compiled. The quaternary watershed level was chosen as the spatial unit for this study because it encompasses the main channel and all connected tributaries, and because Gibson (2006) found that watershed-level variables were better predictors of stream fish assemblages in southern Ontario than site-level variables. The quaternary watershed boundary layer is based on a 1:10 000 resolution digital elevation model of southern Ontario (Water Survey of Canada 1977). The stream layer has a resolution of 1:10 000 and is a polyline layer (Ontario Ministry of Natural Resources 2002). The quaternary watershed and stream layer were joined in ArcView GIS (version 3.3; Environmental Systems Research Institute, Inc. 2002).

To assess the thermal diversity of the fish community in each watershed, observations of species caught at unique sampling sites were compiled from several agencies in southern Ontario. Only extensively sampled watersheds were chosen for our study so we could be confident that we had a complete picture of the fish community and its thermal diversity. To determine if watersheds are effectively sampled, Smith and Jones (2005) recommend generating species accumulation curves from random sampling sites stratified by stream order. We generated species accumulation curves from the available site-level data for each watershed using EstimateS software (Colwell 2005). The site data were randomized 1000 times without replacement, and the average number of species found per site sampled was calculated. Randomization is recommended for patchily distributed organisms such as fishes to remove effects of sample order and heterogeneity among samples (Smith and Jones 2005). The first-order jackknife and Chao estimators were used to generate the accumulation curves. We chose two estimators because although there is no singly accepted estimator, these two perform better than other estimators (Walther and Moore 2005). Watersheds with species accumulation curves that did not asymptote were removed from the analysis. This left 43 watersheds for our analysis.

For each watershed, we determined the number of sample sites needed to capture the entire fish community from the jackknife and Chao curves as the point at which the estimated number of species equalled the observed number of species for at least two consecutive sites (Peterson and Slade 1998). If this value differed between the two estimators, the average was used. These values were then used to randomly select sites (stratified by stream order) from the available data in each watershed. Sampling efforts of 0.13–3.02 sites per 10 $km^2$ of quaternary watershed area were required to effectively sample the watersheds (Fig. 1).

The site-level fish data were collected during the summer when the heterogeneity in stream temperatures and separation of thermal habitats are most pronounced. Thus, the site-

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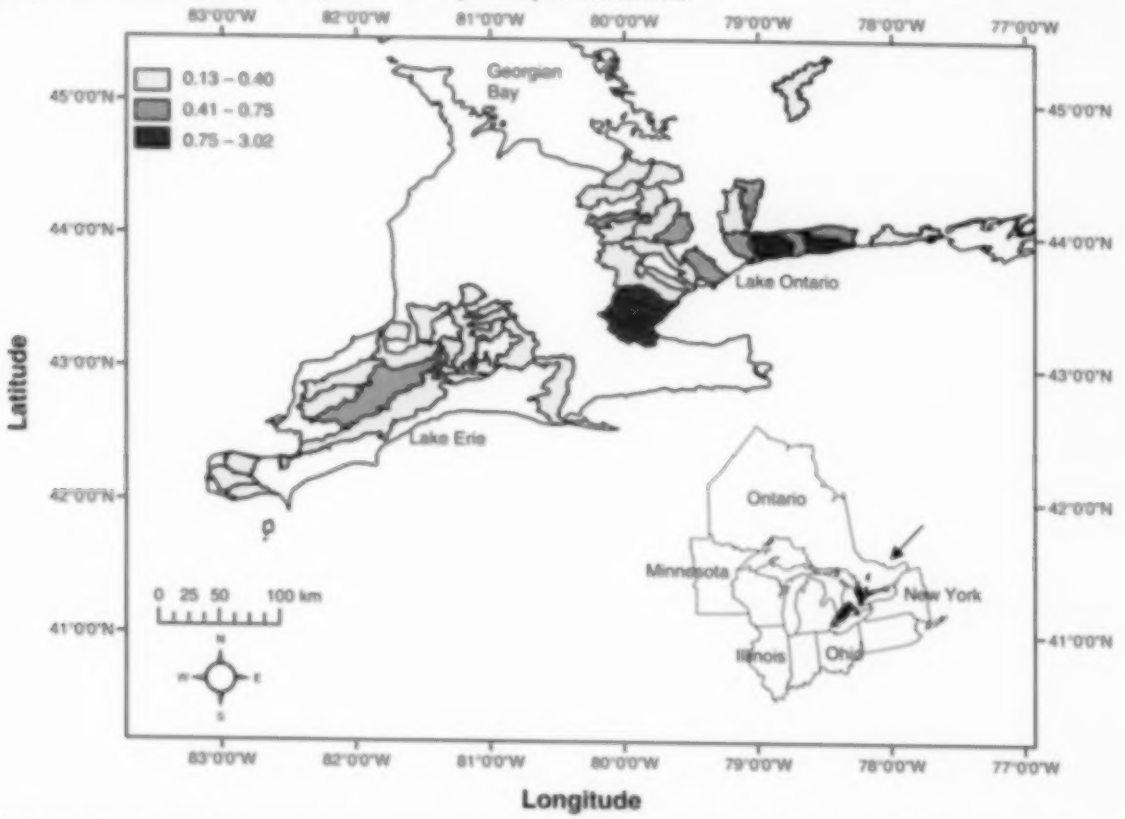
**Fig. 1.** Quaternary watersheds used to determine the influence of air temperature and groundwater on the thermal diversity of stream fish communities in southern Ontario. Shaded watersheds represent the study area, differences in shading represent different levels of sampling effort (number of sample sites per 10 km$^2$ of quaternary watershed area).




level fish data reflected the greatest expression of thermal preferences. Multiple gear types were used throughout each watershed, and although each gear type may be potentially biased for certain species, we assumed that pooling data from all of the gear types provided a complete picture of the fish community in each watershed.

Eighty-one percent of the site-level fish data spanned 1995–2005, with 98% of the data collected from 1970 to 2005. The remaining 2% were collected between 1920 and 1969. Only recent data, 2000–2005, were used for fishes that have been identified as species at risk by the Committee on the Status of Endangered Wildlife in Canada (2006) because their national or global ranges are declining. This minimized the possibility that their current ranges would be overestimated by the inclusion of older data.

Introduced and invasive species such as brown trout (*Salmo trutta*) and common carp (*Cyprinus carpio*) were removed because they did not naturally colonize southern Ontario, they may still be expanding throughout Ontario, and their establishment in these regions may produce an erroneous view of the natural fish assemblages in the watersheds.

Lentic species such as cisco (*Coregonus artedii*) and lake trout (*Salvelinus namaycush*), which may have been caught at locations close to the outlets of lakes, were removed from the data because they dwell in lakes for most, or all, of their life cycle. Lentic or lotic preferences were determined using Coker et al. (2001) and unpublished catch data (N.E. Mandrak, Great Lakes Laboratory for Fisheries and Aquatic Sciences, Fisheries and Oceans Canada, 867 Lakeshore Road, Burlington, ON L7R 4A6).

Once the species lists were generated for each sampling site, Coker et al. (2001) was used to determine the thermal preferences of each species caught at each site in each watershed. Coker et al. (2001) assigned thermal preferences to 207 freshwater fishes in Canada using the best available preferred summer temperatures data. Species were grouped into cold-, cool-, and warm-water temperature guilds with preferences of <19 °C, 19–25 °C, and >25 °C, respectively (Coker et al. 2001). Species ($n$ = 34) that fell into multiple thermal guilds (cold–cool or cool–warm) were excluded from our analyses because these designations indicated that discrepancies exist in the available thermal preferences data for those species, and thus, their actual thermal preferences are unknown.

After removing the lentic, introduced, invasive, and cold–cool and cool–warm species, a pool of 132 species with known thermal preferences was used to describe the possible thermal diversity of the native fish community in each watershed. The thermal diversity of each watershed was then calculated using three metrics, the proportion of sites within a watershed with (*i*) cold-, (*ii*) cool-, and (*iii*) warm-water species. We assessed the effect of sampling effort on the

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**Table 1.** Base-flow index (BFI) developed by Neff et al. (2005) used to represent groundwater discharge potential of different quaternary geology types.

| Quaternary geology type | Example of geological material | BFI value |
|---|---|---|
| Bedrock | Undifferentiated carbonate and clastic sedimentary rock, exposed at surface or covered by a discontinuous, thin layer of drift | 0.586 |
| Coarse | Gravel, sand, silt, and clay, deposited on modern flood plains | 0.821 |
| Fine | Silt and clay, minor sand, basin and quiet water deposits | 0.098 |
| Organic | Peat, muck, and marl | 0 |
| Till | Silty clay to clay matrix, moderate to high matrix carbonate content, clast poor | 0.329 |

**Note:** Higher values indicate greater base flow and likely greater groundwater discharge.

**Table 2.** Descriptive statistics of the air temperature and base-flow variables used to examine the thermal diversity of stream fishes in 43 watersheds throughout southern Ontario.

| Watershed variable | Abbreviation | Minimum | Mean | Maximum | Candidate model[a] |
|---|---|---|---|---|---|
| Mean base-flow index value | BFIMEAN | 0.14 | 0.41 | 0.70 | 1, 2 |
| Coefficient of variation in base-flow index value | BFICV | 0.22 | 0.55 | 1.14 | 1, 2 |
| Maximum annual air temperature (°C) | MAXT | 25.69 | 26.59 | 28.27 | 1 |
| Coefficient of variation in maximum annual air temperature throughout watershed (°C) | MAXTCV | 0 | 0.01 | 0.03 | 1 |
| Mean air temperature (°C) | MAAT | 5.12 | 7.73 | 10.29 | 2 |
| Coefficient of variation in mean annual air temperature throughout watershed (°C) | MAATCV | 0.01 | 0.04 | 0.11 | 2 |
| Log(watershed area) ($km^2$) | LAREA | 1.75 | 2.68 | 3.25 | 1, 2 |

[a]A Pearson correlation matrix identified that the maximum and mean annual air temperature variables were highly correlated; therefore these variables were separated into two regression models (variables in model 1: BFIMEAN, BFICV, MAXT, MAXTCV, LAREA; variables in model 2: BFIMEAN, BFICV, MAAT, MAATCV, LAREA).

thermal diversity metrics by regressing effort (number of sampling sites per 10 $km^2$ of quaternary watershed area) against the number of cold-, cool-, and warm-water species occurring in each watershed.

Spatial models of maximum annual (MAXT) and mean annual (MAAT) air temperature were developed by the Canadian Forest Service at a resolution of 30 arcseconds, or approximately 1 km, following the methods in Price et al. (2000) and McKenney et al. (2006*a*). The spatial models were generated using 30-year climate normals data spanning 1971–2000 (Meteorological Service of Canada 2004) and ANUSPLIN (McKenney et al. 2006*a*). ANUSPLIN is a suite of programs used to produce spatial climate models by interpolating among a network of point climate station latitude, longitude, and elevation data using thin plate smoothing spline algorithms (McKenney et al. 2006*a*). Maximum and mean annual air temperatures were chosen because they have been previously linked to fish species richness in streams (Rathert et al. 1999; Mohseni et al. 2003).

An existing base-flow index (BFI) developed by Neff et al. (2005) was used to represent groundwater discharge in the watersheds. This index represents the long-term average rate of base flow relative to the long-term average rate of total stream flow in five classifications of the quaternary geology, namely, course- and fine-textured sediments, till, shallow bedrock, and organic deposits (Neff et al. 2005). The index ranges from 0–0.82, with higher BFI values indicating greater base flow (Table 1). The BFI values for the five geology types were joined to the existing quaternary geology layer for Ontario to produce a seamless map of what is estimated to be BFI due to groundwater discharge.

The quaternary watershed boundaries were overlaid onto the maximum annual air temperature, mean annual air temperature, and BFI layers, and zonal statistics in ArcView GIS (version 3.3; Environmental Systems Research Institute, Inc. 2002) were used to summarize the air temperature and groundwater variables (Table 2).

### Statistical analyses

Descriptive statistics were calculated for the air temperature and BFI data (Table 2). A Pearson correlation matrix was used to identify highly correlated variables, correlation coefficients ≥0.80 (Franzblau 1958). The correlation matrix indicated that the maximum and mean annual air temperature variables were highly correlated; therefore these variables were separated into two models for the regression analyses (Table 2). Stepwise linear regressions were performed in SPSS for Windows (SPSS Inc. 2003) to determine how much variance in the three thermal diversity metrics could be explained by air temperature and BFI variables. The candidate models with higher $R^2$ values were used in the climate change analyses.

### Climate change scenarios

The International Panel on Climate Change (IPCC) recommends using multiple climate models and emissions scenarios when assessing the potential impacts of climate change (Canadian Institute of Climate Studies 2006); hence, we chose two climate models, the Canadian Global Coupled Model 2 (CGCM2) and the Hadley Centre Coupled Model 3 (HadCM3), and two emissions scenarios, A2 and B2. The CGCM2 uses atmospheric general circulation models cou-

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**Table 3.** Average air temperature variable values for 43 quaternary watersheds in southern Ontario under the Canadian Global Coupled Model 2 (CGCM2) and Hadley Centre Climate Model 3 (HadCM3) climate models with the A2 and B2 emissions scenarios for years 2025 and 2055.

| | | CGCM2 A2 | | CGCM2 B2 | | HadCM3 A2 | | HadCM3 B2 | |
|---|---|---|---|---|---|---|---|---|---|
| Air temperature variable | Present | 2025 | 2055 | 2025 | 2055 | 2025 | 2055 | 2025 | 2055 |
| MAXT | 26.59 | 28.38 | 29.07 | 28.00 | 28.75 | 28.51 | 30.73 | 28.34 | 29.82 |
| MAXTCV | 0.01 | 0.01 | 0.01 | 0.01 | 0.01 | 0.01 | 0.01 | 0.01 | 0.01 |
| MAAT | 7.73 | 8.81 | 10.36 | 8.86 | 9.72 | 8.40 | 9.76 | 8.31 | 9.42 |
| MAATCV | 0.04 | 0.04 | 0.03 | 0.04 | 0.03 | 0.04 | 0.03 | 0.04 | 0.03 |

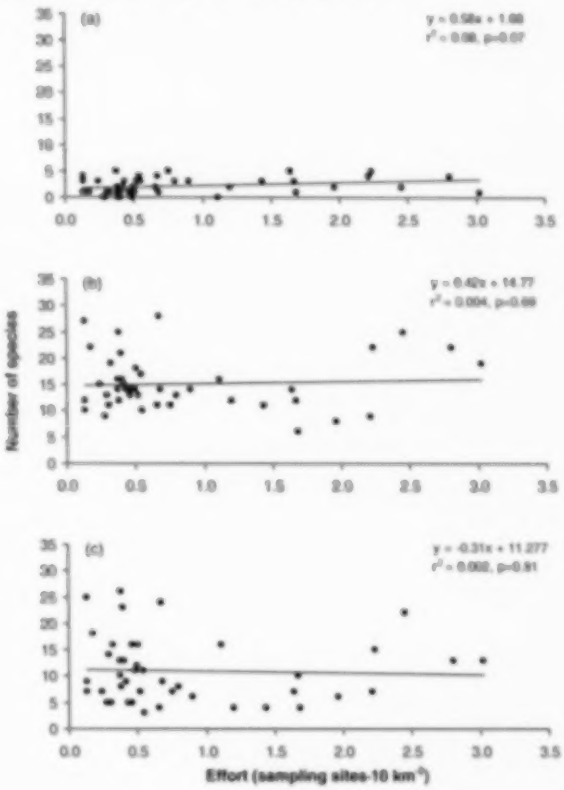
**Note:** MAXT, maximum annual air temperature; MAAT, mean annual air temperature; MAXTCV and MAATCV, coefficient of variations in MAXT and MAAT, respectively.

pled with three-dimensional oceanic models and has a spatial resolution of 3.75° latitude and longitude, approximately 400 km × 400 km at the equator. The HadCM3 also uses a coupled atmosphere–ocean general circulation model that has a resolution of 2.5° latitude × 3.75° longitude, which produces a resolution of 295 km × 278 km at 45° latitude on land. Both models use variables such as solar radiation, terrestrial thermal radiation, water vapour, ozone, freezing and melting of soil moisture, surface runoff, soil drainage, vapour pressure, snow depth, vegetation, precipitation, and cloud cover to model future climates (Canadian Institute of Climate Studies 2006). The A2 emissions scenario represents a world with regionally focused economic growth with a continuously increasing global population. The B2 emissions scenario represents a more social and environmental focus with less rapid economic growth. The A2 and B2 scenarios predict increases in temperatures of 3.8 and 2.7 °C, respectively, by 2100 (Canadian Institute of Climate Studies 2006). Emissions scenarios represent a suite of future conditions given our current understanding of greenhouse gas and climate dynamics, the latest information on economic restructuring throughout the world, rates, trends in technological change, and a range of different economic-development pathways (Canadian Institute of Climate Studies 2006).

Spatial models of the maximum and mean annual air temperatures under the CGCM2 A2, CGCM2 B2, HadCM3 A2, and HadCM3 B2 scenarios were provided by the Canadian Forest Service. These models were generated using scenario data from the IPCC distribution centre and the Canadian Centre for Climate Modelling and Analysis (McKenney et al. 2006*b*). The ANUSPLIN tool was employed to create the spatial climate models at a gridded resolution of 1 km. Each spatial climate model was imported into ArcView GIS (version 3.3), and zonal statistics were used to calculate the changes in mean and maximum annual air temperatures in each watershed in 2025 and 2055 (Table 3). These data were then entered into the regression models to determine how the distributions (proportion of sites within the watersheds) of the cold-, cool-, and warm-water thermal guilds may change with climate.

The BFI used in this study as an indicator of groundwater discharge is not likely to substantially change with climate because it is primarily a function of geology. Climate change will undoubtedly affect different properties of groundwater, such as the quantity and timing of discharge (Croley and Luukkonen 2003; Piggott et al. 2005), but the potential changes in groundwater temperatures and fish habitat may take decades or centuries to be realized (A.R. Piggott, personal observation). As a result, the BFI values of the watersheds were not altered in our climate change analyses.

**Fig. 2.** Number of (*a*) cold-, (*b*) cool-, and (*c*) warm-water species caught at different sampling efforts (number of sampling sites per 10 km$^2$ of quaternary watershed area) throughout 43 quaternary watersheds in southern Ontario.




## Results

### Watersheds and thermal guilds

The 43 watersheds used in this study ranged in size from 56 to 1764 km$^2$ (Table 2). Species richness ranged from 11–56 species, with 0–5 cold-water, 6–28 cool-water, and 3–26

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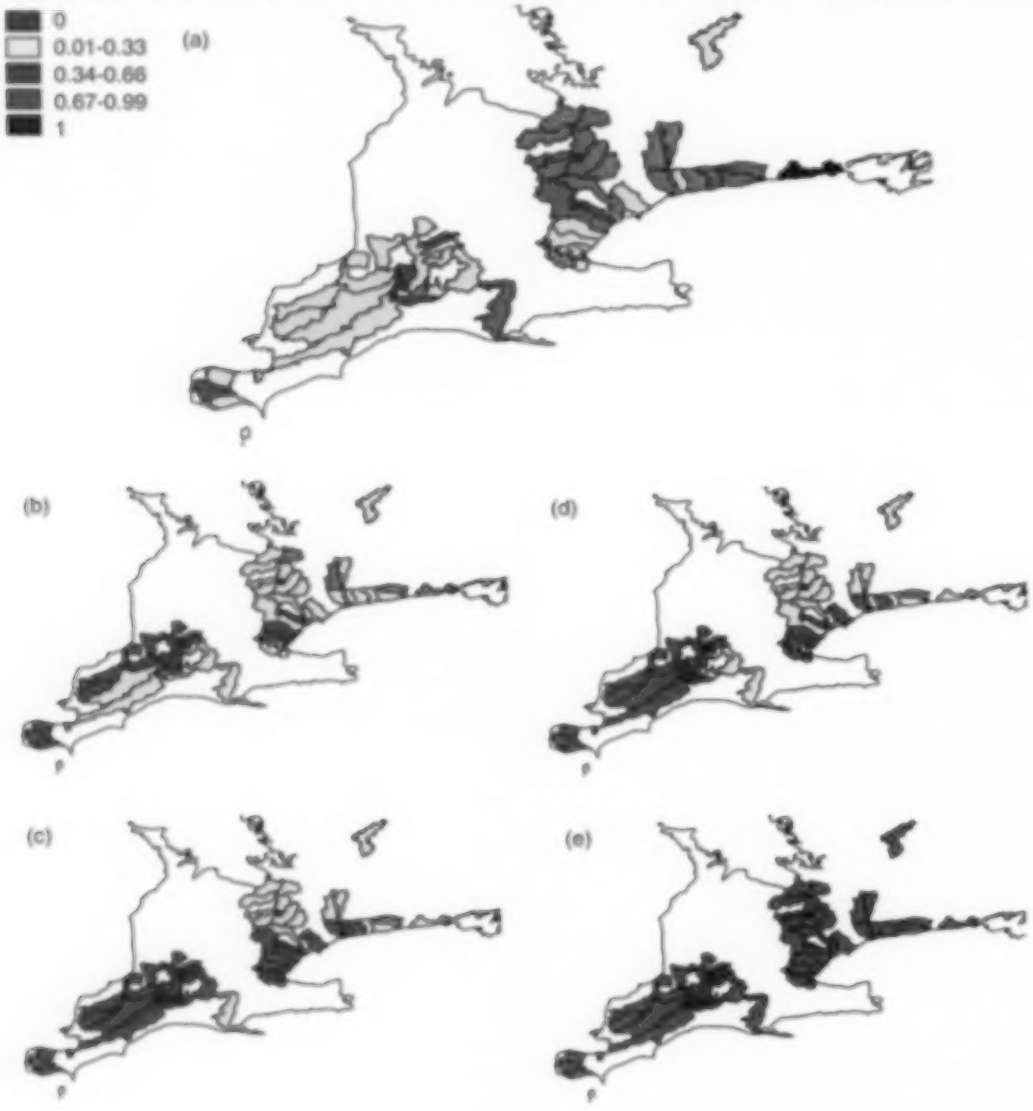
**Fig. 3.** Proportion of sites in 43 southern Ontario watersheds having cold-water fishes: (*a*) currently; (*b*–*e*) under the climate scenarios that showed the least and greatest impact on cold-water fish distributions, the Canadian Global Climate Model 2 (CGCM2) B2 ((*b*) 2025 and (*c*) 2055) and the Hadley Centre Climate Model 3 (HadCM3) A2 ((*d*) 2025 and (*e*) 2055), respectively.




warm-water species within an individual watershed. Regressions of sampling effort against the number of species in each thermal guild and watershed indicated that there was no significant effect of effort on the number of cold-water ($F_{0.05(1),1,41} = 3.47$, $p = 0.07$), cool-water ($F_{0.05(1),1,41} = 0.16$, $p = 0.69$), or warm-water ($F_{0.05(1),1,41} = 0.06$, $p = 0.81$) species caught in the watersheds (Fig. 2).

Cold-water species occurred in a greater proportion of sites throughout the southeastern regions than the southwestern regions of our study area, with the exception of the Big Creek watershed that flows into Lake Erie (Fig. 3). Shelter Valley Creek was the only watershed with cold-water species at every site sampled. Cold-water fishes were the dominant thermal guild (only guild occurring in >66% of the sampled sites) in the Willow Creek watershed near Georgian Bay (Table 4). Cool-water fishes were found in every watershed, with 38 of the 43 watersheds having cool-water fishes at >66% of the sampled sites (Fig. 4). Three of these watersheds had both cold- and cool-water species at >66% of the sites (Table 4). These included the Bomanville and Duffins creek watersheds that flow into Lake Ontario and the Big Creek watershed that flows into Lake Erie. Cool-water fishes were the only dominant thermal guild in 8 of the watersheds (Table 4). Warm-water fishes were well distributed throughout all of the watersheds in the western region of the study area but were poorly distributed in watersheds

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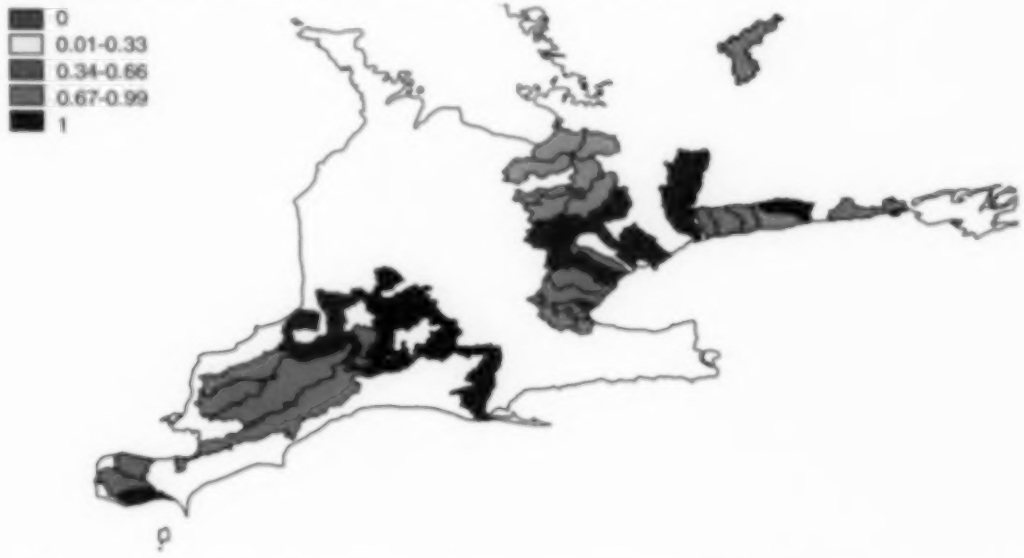
**Table 4.** Average values of the air temperature and groundwater variables of watersheds in southern Ontario having a clearly dominant thermal guild(s) (thermal guild(s) found at >66% of the sites throughout a watershed).

| Thermal diversity | Description | QWS | BFIMEAN | BFICV | MAXT | MAXTCV | MAAT | MAATCV |
|---|---|---|---|---|---|---|---|---|
| Cold | Only cold-water fishes in >66% of sites | 2 | 0.49 | 0.60 | 25.94 | 0.01 | 7.02 | 0.04 |
| Cold–cool | Cold- and cool-water fishes in >66% of sites | 3 | 0.51 | 0.49 | 26.22 | 0.01 | 7.77 | 0.05 |
| Cold–cool–warm | Cold-, cool-, and warm-water fishes in >66% of sites | 3 | 0.61 | 0.41 | 26.25 | 0.01 | 7.34 | 0.06 |
| Cool | Only cool-water fishes in >66% of sites | 8 | 0.49 | 0.49 | 26.44 | 0.01 | 7.22 | 0.04 |
| Cool–warm | Cool- and warm-water fishes in >66% of sites | 24 | 0.34 | 0.60 | 26.88 | 0.01 | 8.26 | 0.03 |
| Warm | Only warm-water fishes in > 66% of sites | 0 | | | | | | |
| No dominant thermal guild | | 3 | 0.53 | 0.52 | 26.12 | 0.02 | 6.80 | 0.06 |

**Note:** QWS, number of quaternary watersheds; BFIMEAN, mean base-flow index value; MAXT, maximum annual air temperature; MAAT, mean annual air temperature; BFICV, MAXTCV, and MAATCV, coefficients of variation in BFI, MAAT, and MAXT, respectively.

**Fig. 4.** Proportion of sites in 43 southern Ontario watersheds having cool-water fishes.




throughout the Nottawasaga region near Georgian Bay and eastern region of our study area (Fig. 5). Although the warm-water fishes were well distributed, they were not the only dominant thermal guild in any of the watersheds (Table 4). Cool- and warm-water fishes were the dominant thermal guilds in 24 watersheds (Figs. 4 and 5). Three watersheds (Credit, Ganaraska, and Shelter Valley) had all three thermal guilds at >66% of the sites sampled (Table 4). Three watersheds in the Nottawasaga region did not have a dominant thermal guild (Table 4).

## Models

Stepwise multiple linear regressions indicated that mean BFI, coefficient of variation in BFI, and maximum annual air temperature explained 53.9% of the variance in the proportion of sites having cold-water species (Table 5). Significant regression models could not be developed for the proportion of sites with cool-water fishes. Mean BFI, maximum annual air temperature, and the coefficient of variation in maximum annual air temperature explained 54.1% of the variance in the proportion of sites having warm-water species (Table 5). The groundwater and air temperature variables had opposite effects on the cold- and warm-water fish distributions within the watersheds. BFI was positively related to cold-water distributions but negatively related to warm-water distributions within the watersheds, whereas maximum air temperature was negatively related to cold-water fish distributions but positively related to warm-water fish distributions.

## Climate change

Model 1 was used to predict the potential impacts of climate change on cold- and warm-water fish distributions

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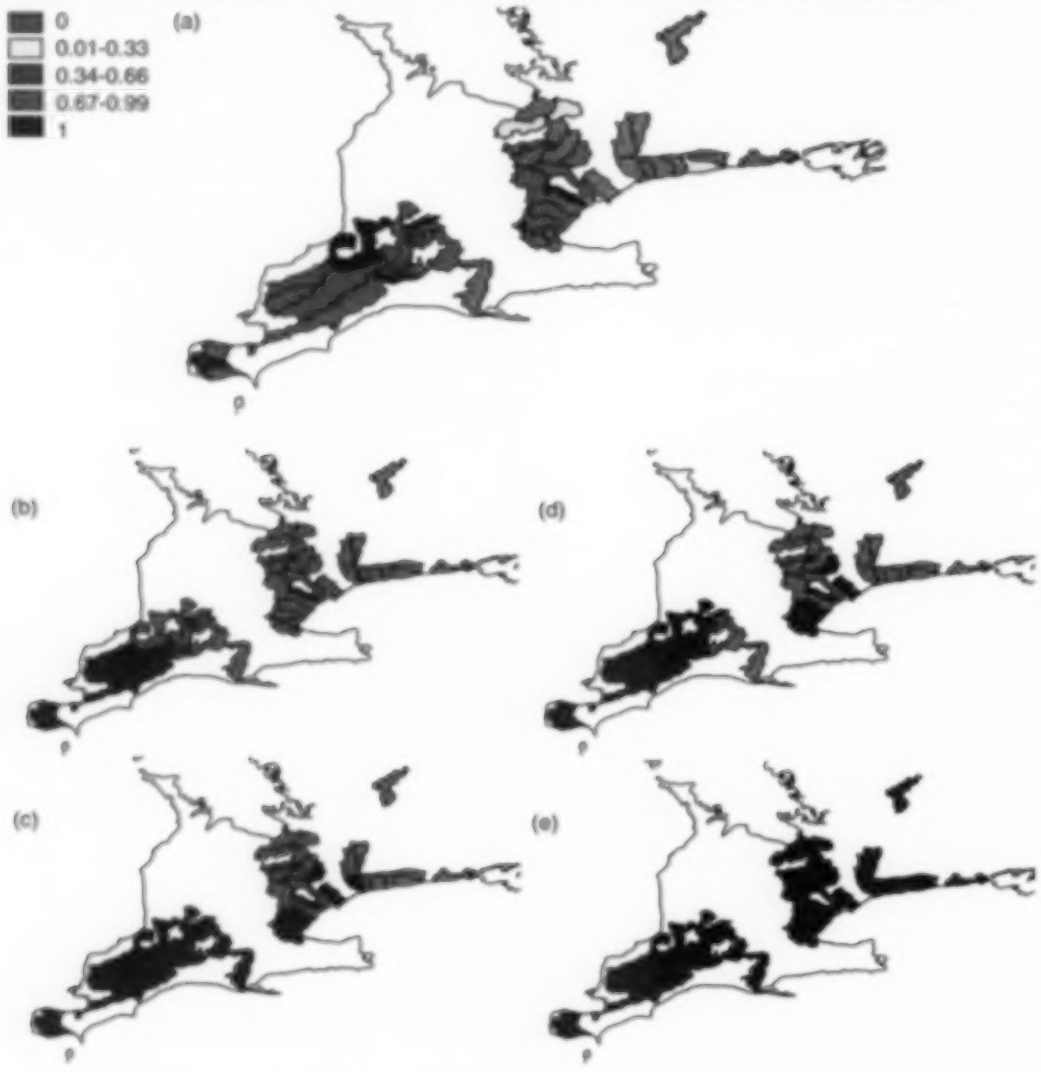
**Fig. 5.** Proportion of sites in 43 southern Ontario watersheds having warm-water fishes: (*a*) currently; (*b–e*) under the climate scenarios that showed the least and greatest impact on warm-water fish distributions, the Canadian Global Climate Model 2 (CGCM2) B2 ((*b*) 2025 and (*c*) 2055) and the Hadley Centre Climate Model 3 (HadCM3) A2 ((*d*) 2025 and (*e*) 2055), respectively.




within the watersheds by entering the climate change scenario data into the models (Table 5). Predicted values greater than 1 that arose when, for example, the forecasted temperatures with climate change were greater than the temperatures used to model the proportion of sites with warm-water species were set to 1; likewise, values less than 0 were set to 0. Climate change impacts on cool-water fishes could not be modelled because a significant regression model could not be developed for them.

In general, climate change reduced the proportion of sites within the watersheds having cold-water species but increased the proportion of sites with warm-water species (Table 6). The HadCM3 scenarios caused greater changes in the cold- and warm-water fish distributions than the equivalent CGCM2 scenarios (Table 6). The A2 scenarios caused greater changes in the thermal diversities of the watersheds than the B2 scenarios (Table 6).

In all of the climate scenarios, cold-water distributions may be reduced to less than 67% of sites sampled within any watershed by 2025 (Table 6). The CGCM2 B2 showed the least reduction by 2055, whereas the HadCM3 A2 scenario predicted the greatest (Table 6; Fig. 3). Under the CGCM2 B2 scenario, cold-water fishes may still be found in 16 of the 43 watersheds by 2055. Watersheds in the eastern region of our study area may have higher proportions of sites with cold-water species than western watersheds (Fig. 3). Under

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**Table 5.** Multiple linear regression results relating air temperature and groundwater discharge to the thermal diversity of stream fishes in 43 southern Ontario watersheds.

| Thermal diversity | Model | Variable | Coefficient | *F* statistic | Standardized β coefficient | $R^2$ |
|---|---|---|---|---|---|---|
| Proportion of sites with cold-water fishes | 1 | CONSTANT | 4.51 | 15.20 | | 0.54 |
| | | BFIMEAN | 1.50 | | 0.63 | |
| | | BFICV | 0.66 | | 0.38 | |
| | | MAXT | –0.19 | | –0.39 | |
| | 2 | CONSTANT | –0.29 | 26.01 | | 0.39 |
| | | BFIMEAN | 1.48 | | 0.62 | |
| Proportion of sites with warm-water fishes | 1 | CONSTANT | –3.05 | 15.29 | | 0.54 |
| | | BFIMEAN | –0.47 | | –0.28 | |
| | | MAXT | 0.15 | | 0.43 | |
| | | MAXCV | –10.5 | | –0.34 | |
| | 2 | CONSTANT | –0.50 | 12.81 | | 0.50 |
| | | BFIMEAN | –0.89 | | –0.53 | |
| | | MAAT | 0.10 | | 0.45 | |
| | | MAATCV | –0.40 | | –0.32 | |

**Note:** Significant regression models could not be developed for the proportion of sites with cool-water fishes. BFIMEAN, mean base-flow index value; MAXT, maximum annual air temperature; MAAT, mean annual air temperature; BFICV, MAXTCV, and MAATCV are the coefficients of variation in BFI, MAAT, and MAXT, respectively, throughout the watersheds.

**Table 6.** Climate change impacts on the proportion of sites having cold- and warm-water fishes by 2025 and 2055 in 43 southern Ontario watersheds under the Canadian Global Coupled Model 2 (CGCM2) and Hadley Centre Climate Model 3 (HadCM3) climate models with the A2 and B2 emissions scenarios for years 2025 and 2055.

| | | | CGCM2 A2 | | CGCM2 B2 | | HadCM3 A2 | | HadCM3 B2 | |
|---|---|---|---|---|---|---|---|---|---|---|
| Thermal guild | Proportion of sites | Present | 2025 | 2055 | 2025 | 2055 | 2025 | 2055 | 2025 | 2055 |
| Cold | 0 | 6 | 21 | 29 | 15 | 27 | 22 | 43 | 19 | 39 |
| | 0.01–0.33 | 19 | 20 | 14 | 24 | 15 | 20 | 0 | 24 | 4 |
| | 0.34–0.66 | 10 | 2 | 0 | 4 | 1 | 1 | 0 | 0 | 0 |
| | 0.67–0.99 | 7 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Warm | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| | 0.01–0.33 | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| | 0.34–0.66 | 13 | 0 | 0 | 3 | 0 | 0 | 0 | 1 | 0 |
| | 0.67–0.99 | 22 | 23 | 11 | 31 | 16 | 22 | 0 | 24 | 4 |
| | 1 | 5 | 20 | 32 | 9 | 27 | 21 | 43 | 18 | 39 |

the HadCM3 A2 scenario, none of the watersheds in our study area may have cold-water species by 2055 (Table 6; Fig. 3).

Warm-water fish distributions may increase with climate change. The HadCM3 A2 showed the greatest increase and the CGCM2 B2 showed the smallest increase by 2055 (Table 6; Fig. 5). Under the CGCM2 B2 scenario, all of the watersheds in the western region of our study area may have warm-water fishes at every site sampled (Fig. 5). Watersheds in the Nottawasaga region and most eastern watersheds may have warm-water fishes at >66% of the sites sampled by 2055. The HadCM3 A2 climate scenario suggests that warm-water fishes may occur at 100% of sampled sites by 2055 (Table 6; Fig. 5). The CGCM2 B2 scenario suggests that warm-water species may be the dominant thermal guild (occurring at >66% of the sites) in most of the southern Ontario watersheds by 2055 (Figs. 3 and 5). However, watersheds in the Nottawasaga region and eastern Lake Ontario basin may contain the most thermally diverse fish communities in 2055 as cold-water species may occur in up to 66% and warm-water species in up to 100% of any sampled sites in those watersheds (Figs. 3 and 5). The HadCM3 A2 predicts a less diverse future with the complete loss of the cold-water thermal guild but expansion of the warm-water guild in all of the watersheds by 2055.

Using the BFI, maximum annual air temperatures, and CGCM2 B2 scenario results, we developed a simple index of the likelihood of each of the watersheds in southern Ontario retaining cold-water species after climate change (Table 7). This index represents the best case or least impacted scenario for cold-water fishes. We assumed that warmwater species distributions will remain the same or increase within each watershed with climate change and, therefore, focused on cold-water species. The likelihood map showed a latitudi-

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**Table 7.** Average current conditions of groundwater discharge (BFI) and maximum annual air temperature (MAXT) for watersheds that either retained or lost cold-water species after the 2055 Canadian Global Coupled Model 2 B2 climate scenario.

| | | | Likelihood to retain cold-water species index | | |
|---|---|---|---|---|---|
| | Watersheds with cold-water species in 2055 | Watersheds without cold-water species in 2055 | Low | Mid | High |
| BFIMEAN | 0.54 | 0.36 | <0.36 | >0.36 < 0.54 | >0.54 |
| MAXT | 26.07 | 26.90 | >26.9 | <26.9 > 26.07 | <26.07 |

**Note:** The current conditions were then used to develop a likelihood index of southern Ontario watersheds to retain cold-water fishes after climate change from combinations of current groundwater discharge and air temperature conditions.

**Fig. 6.** Likelihood index that quaternary watersheds in southern Ontario may retain cold-water species after climate change.

nal gradient with watersheds in the northern region of southern Ontario likely to retain cold-water species, whereas watersheds in the southern region are likely to lose cold-water species with climate change (Fig. 6).

## Discussion

Groundwater and air temperature variables explained a significant amount of the cold- and warm-water thermal diversity within the sampled watersheds. Mean BFI was positively related to cold-water fish distributions but negatively related to warm-water fish distributions, whereas the inverse was true for maximum annual air temperature. This can be attributed to the influence of groundwater and air temperature on the availability of suitable thermal habitat for fishes. Groundwater discharge into a stream may decrease stream temperatures in the summer, whereas high air temperatures increase stream temperatures in the summer. These results are consistent with those of previous studies (Wichert and Lin 1996; Wang et al. 2003; Gibson 2006).

Wichert and Lin (1996) developed the weighted species association tolerance index with respect to water temperature (WSATI-WT) to examine the thermal diversity of stream fish communities near Toronto, Ontario. They found a positive relationship between WSATI-WT and maximum summer stream temperatures: as maximum summer temperatures increased, so did the relative abundance of warm-water fishes in the streams. The WSATI-WT approach was not applied in our study because it was developed for 60 species and we were dealing with a species pool (after removal of nonnative species) of 132 species. The WSATI-WT also requires specific preferred, optimal, and upper lethal temperature data that were not available for all of the other 72 species in Ontario. Cold-water fish assemblages in 79 watersheds in northern Michigan, Wisconsin, and Minnesota were positively associated with groundwater delivery rate and narrow, deep, high-gradient (steep) streams (Wang et al. 2003). Gibson (2006) found that fish assemblage patterns of 196 watersheds (defined in that study as drainage area upstream of a fish sampling site along the stream continuum) in southern Ontario were best described by watershed-level BFI and biogeography.

The groundwater and air temperature variables did not explain any variance in the cool-water fish distributions because cool-water fishes were abundant throughout all of the watersheds. Cool-water fishes were found in >80% of the sites in 36 of the 43 watersheds. This made it difficult to detect a pattern in cool-water fish distributions and suggests that suitable thermal habitat is abundant for cool-water fishes in many of the watersheds. Although we were not able to ex-

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amine potential climate change impacts on cool-water fishes, previous studies have found that cool-water habitat in streams may decrease with climate change (Mohseni et al. 2003).

The regression and the CGCM2 A2, CGCM B2, and HadCM3 B2 scenarios suggest that watersheds with high groundwater discharge offer not only more suitable thermal habitat for cold-water fishes, but also may lessen climate change impacts on cold-water species. These watersheds, located in the Nottawasaga region and eastern Lake Ontario basin, may also contain the most thermally diverse fish communities as both cold- and warm-water species may be caught at sampling sites within those watersheds in the future.

Our findings suggest that two management approaches may be taken. Watersheds in which thermal diversity is at risk in the short term (e.g., watersheds with low BFI) may be given high conservation priority. Alternatively, if we treat climate change as an inevitability, watersheds with high BFI may be given high conservation priority because they will naturally offer more suitable habitat and thermal refugia for cold-water fishes in the future. In both cases, anthropogenic impacts on the thermal habitat of these watersheds should be minimized. This may be accomplished by placing restrictions on ground- and surface-water withdrawals (Ontario Ministry of the Environment 2004), increasing forest canopy and riparian vegetation to counteract increasing air and stream temperatures (Lyons et al. 2000; Gaffield et al. 2005), and regulating urban development to minimize cumulative stresses on ground- and surface-water quantity and quality (Paul and Meyer 2001).

### Limitations of this approach and next steps

The BFI used in this study represents an approximation of groundwater discharge into a stream. The relationships uncovered in this study are partially attributable to improved stream flow conditions in watersheds with higher BFI. During periods of low flow, more groundwater discharge may not only improve thermal conditions, but may also increase the volume of water and, consequently, suitable habitat for fishes. Climate change induced differences in precipitation and temperature that may influence the magnitude and timing of groundwater discharge should be addressed in future analyses.

It should be noted that our approach implies that air temperature and groundwater variable values represent average conditions across the watersheds, whereas the values of these variables at the individual fish sampling sites may reflect conditions across only a portion of the watershed in some cases and across one or more upstream watershed(s) in other cases. This assumption, which was necessary to enable the analyses described in this paper, may be a potential source of some of the uncertainty in relating the thermal diversities within the watersheds to the average properties of the watersheds. Delineation of watersheds upstream of the sample sites would provide a more detailed examination of the BFI and air temperature conditions influencing the thermal guilds found at unique sites, but these data are not currently available for all of the watersheds used in our analyses.

This study does not include all of the variables that influence the thermal habitat and fish diversity in streams: variables such as flow, dissolved oxygen concentration, channel morphometry, riparian vegetation, and interspecific interactions (Poole and Berman 2001; Jackson and Mandrak 2002; Wang et al. 2003). The number of variables was purposely trimmed to assess the direct impacts of the main variables identified as drivers of stream temperature and thermal habitat. Future research should incorporate the biotic interactions (intraspecific and interspecific) and other abiotic variables that may influence the thermal diversities of fish communities within the watersheds.

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# Stocking success of local-origin fry and impact of hatchery ancestry: monitoring a new steelhead (*Oncorhynchus mykiss*) stocking program in a Minnesota tributary to Lake Superior

**David C. Caroffino, Loren M. Miller, Anne R. Kapuscinski, and Joseph J. Ostazeski**

**Abstract:** The inception of a hatchery program to rebuild a naturalized steelhead (*Oncorhynchus mykiss*) population in Minnesota waters of Lake Superior gave us the rare opportunity to monitor the success of fry stocking and determine if hatchery ancestry can reduce fitness of stocked fish in the early generations of a stocking program. Through genetic monitoring of two year classes, we determined that hatchery adults produced 1.3–6.2 times as many age-2 juveniles per female than naturally spawning fish. Survival of stocked fry of parents born in a hatchery relative to those of parents born in the wild was 70% in paired-stocking comparisons. These results suggest that stocking local-origin fry can increase the short-term abundance of depleted populations and that fish with no hatchery history are a better source for supplemental stocking. Additionally, sampling small numbers of adults for broodstock created genetically distinct groups, which could potentially cause long-term genetic change in the population. Genetic monitoring of adults will be essential to determining whether differences observed persist through the life cycle of the stocked fish.

**Résumé :** La mise en marche d'un programme de pisciculture pour restaurer une population naturalisée de truites arc-en-ciel anadromes (*Oncorhynchus mykiss*) dans les eaux du lac Supérieur au Minnesota nous a fourni une occasion unique de suivre le succès de l'alevinage et de déterminer si l'ascendance en pisciculture peut réduire la fitness des poissons ensemencés durant les premières générations d'un programme d'empoissonnement. Lors d'un suivi génétique de deux classes d'âge, nous avons déterminé que les adultes de pisciculture produisent 1,3 à 6,2 fois le nombre de jeunes d'âge 2 par femelle que les poissons qui fraient de manière naturelle. Dans des comparaisons appariées d'empoissonnement, la survie des alevins ensemencés dont les parents sont nés en pisciculture représente 70 % de celle des alevins dont les parents sont nés en nature. Ces résultats indiquent que des empoissonnements avec des alevins d'origine locale peuvent augmenter à court terme l'abondance des populations épuisées et que les poissons sans antécédent en pisciculture sont une meilleure source pour les empoissonnements complémentaires. De plus, le prélèvement de petits nombres d'adultes pour former les stocks reproducteurs crée des groupes génétiquement distincts qui peuvent potentiellement causer des changements génétiques à long terme dans la population. Il est donc nécessaire de faire un suivi génétique des adultes afin de déterminer si les différences observées persistent tout au long du cycle biologique des poissons ensemencés.

[Traduit par la Rédaction]

## Introduction

Salmonid hatcheries have been used in various roles since the mid-1800s (Schramm and Piper 1995). Hatchery fish have been stocked in many locations and at various life stages, all in the hope of increasing local populations (Steward and Bjornn 1990). Monitoring of such stockings is imperative to determining their success or failure and the effects they have on natural populations (Winton and Hilborn 1994; Miller and Kapuscinski 2003; Brannon et al. 2004).

Many studies have evaluated the fitness of hatchery fish relative to native stocks, and inferior performance is a common result. Hatchery fish of a nonlocal origin often experience reduced survival and do not significantly contribute to natural populations (e.g., Chilcote et al. 1986; Kostow et al. 2003; McLean et al. 2003). These introduced fish lack al-

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leles adapted to the local environment, a likely major reason for their reduced survival. In addition to poor performance throughout their life cycle, hatchery fish of a different genetic origin may threaten native stocks through outbreeding depression (Miller and Kapuscinski 2003; Miller et al. 2004).

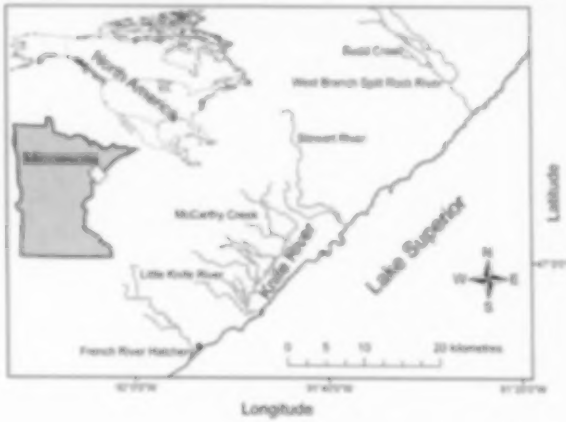
Fewer studies have evaluated supplemental stocking when a local-origin broodstock is used. Most of the research of this type has focused on a local broodstock that had been propagated in a hatchery for multiple generations (Reisenbichler and McIntyre 1977; Fleming et al. 1997; Dannewitz et al. 2003). Hatchery fish of a common genetic origin were more successful than nonlocal broodstocks, but still often experienced reduced survival compared with that of wild fish.

Domestication selection may explain why even local broodstocks with hatchery ancestry exhibit poor survival in the wild. Domestication refers to any change in the selection regime of a cultured population relative to that experienced by the natural population (Waples 1999). Bringing fish into an artificial environment for a part of their life exposes them to different selective pressures than would be encountered in the wild in terms of both survival and mate selection (Busack and Currens 1995). In one less-considered component of domestication selection, the hatchery environment relaxes the natural process of selection and allows some individuals to survive that otherwise would not have (Waples 1999). The offspring of hatchery fish, therefore, may experience poor survival in the wild due to inheritance of traits that are maladapted to the natural environment.

It is unclear how much hatchery ancestry is required to reduce survival of locally adapted fish. Berejikian and Ford (2004) reviewed the current literature and found only one (unpublished) study (Blouin 2003) that examined a first-generation hatchery stock. That work, later published in Araki et al. (2007*a*) and extended in Araki et al. (2007*b*), found that although supplementation was initially considered successful, locally derived hatchery steelhead (*Oncorhynchus mykiss*) experienced reductions in reproductive success relative to wild fish over the first two generations of the hatchery program. The lack of data indicates the rarity of opportunity and ability to monitor fish stocking programs from their inception. Such an opportunity to monitor a stocking program existed in the Minnesota portion of Lake Superior as the Minnesota Department of Natural Resources (MNDNR) initiated a steelhead stocking program.

In Minnesota, declining steelhead populations in tributaries to Lake Superior have led the MNDNR to begin a supplemental stocking program using local broodstock with limited hatchery experience. Steelhead were first introduced into Lake Superior in the late 1800s (MacCrimmon and Gots 1972) and first reached Minnesota waters in 1895 (Hassinger et al. 1974). They have since established genetically distinct populations spawning within the various tributaries along the shore (Krueger et al. 1994). The habitat in this area is characterized by steep slopes, and often barrier waterfalls occur a short distance upstream from Lake Superior. Nearly half of the entire spawning and nursery habitat accessible to steelhead in Minnesota waters is found in the Knife River and its tributaries (Fig. 1; Schreiner 2003). It is thought that historic spawning runs in this river included at least 1000 individuals; however, the current number of spawners is between 200 and 400 adults as factors such as harvest, stream

**Fig. 1.** Map of the southern portion of the Minnesota north shore of Lake Superior, showing only those rivers used in this study.




degradation, and fish community changes in Lake Superior have likely reduced the annual migration. Declining populations since the 1970s led to a period of stocking both local and nonlocal steelhead fry. Although the success of these stockings was never directly evaluated, the Knife River population failed to recover. To protect the remaining spawning population, the harvest fishery for steelhead in the Knife River was closed in the mid-1990s.

The 1996 construction of an adult and juvenile trap less than 1 km upstream of the mouth of the Knife River now allows monitoring of the population as both down-migrating juveniles and up-migrating adults. This makes it possible to distinguish between stream and lake sources of mortality and provides an accurate estimate of both the adult and juvenile populations (Schreiner 2003). The length of time that juvenile steelhead spend in the river depends on environmental conditions and density of fish in the stream. Age-0 emigrants experience nearly 100% mortality and have not been found to recruit to spawning age. Steelhead migrating at age 1 are smaller than age-2 migrants (1997–2004 mean difference 5.0 cm; J.J. Ostazeski, unpublished data) and have a mean survival rate of 0.25%, making their contribution to the population largely dependent on the size of the emigrating class. Most steelhead that move into Lake Superior before age 2 have not undergone smoltification and purposely migrated, but rather ended up in the lake as a result of natural movement in short-run streams (Negus 2003). Fish emigrating at age 2 are of most interest to managers as roughly 80% of adults that return to spawn migrated to Lake Superior as age-2 juveniles (Hendrickson 2004). The operation of both traps makes it possible to carefully monitor the success of a stocking program, measured by the number of age-2 juveniles produced.

A new hatchery program began after construction of the adult trap in 1996. Using only naturalized steelhead captured at the Knife River adult trap as broodstock, the MNDNR biannually stocked age-1 juveniles beginning in 1997. Each age-1 steelhead stocked upstream in the Knife River had a fin clipped for later identification as a hatchery-born fish. Some of these stocked age-1 fish survived and returned to the Knife River as adults in spawning condition. When cap-

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tured moving upstream to spawn, none of the hatchery-born steelhead was passed above the adult trap, but all were returned to the hatchery as broodstock.

The success of this age-1 stocking program was low, with adult return rates around 1% (Ward 2004). The high cost of production and poor recruitment of the stocked age-1 juveniles shifted recovery plans to include a focus on fry stocking. In 2002, fry produced from the hatchery-born, clipped adults captured at the Knife River trap were stocked into upstream areas of the Knife River. In 2003, fry from both hatchery-born and natural-born adults were stocked into the Knife River.

Our primary objective was to evaluate the effectiveness of fry stocking in increasing the number of age-2 emigrants. Secondarily, we compared the survival of fry of parents born in the hatchery with fry of parents born in the wild. This allowed us to examine the rate at which domestication selection could affect this population. In addition, data collected for these objectives allowed us to evaluate another potential consequence of hatchery propagation: a shift in the genetic composition of hatchery subpopulations due to the use of a limited number of adults for hatchery spawning.

## Materials and methods

We addressed our primary objective by collecting samples from steelhead at the Knife River fish traps during 2002–2005. Scale samples were taken from adult steelhead when they were captured during their upstream spawning migration in 2002 and 2003. Some adults were passed upstream to spawn naturally, and the rest were taken to the hatchery for spawning. Fry were then stocked into upstream areas of the Knife River. Scale samples were collected from age-1 juveniles during their down-migration in 2003 and 2004 and from age-2 juveniles during 2004 and 2005. Because the stocked fry were not marked in any way, we used DNA-based parentage analysis to determine if the sampled juveniles belonged to a hatchery group or were naturally reproduced in the stream.

In this paper, we refer to the success of stocking in terms of an increase in the average family size of adult female steelhead. For a stocking program to succeed, a female in the hatchery must have a larger family size than she would if she were spawning naturally. In 2002, more than one male was mated with some females, thus families are considered as all offspring with a common mother. Family size was measured at the age-1 and age-2 stages.

We conducted a separate paired-stocking experiment to determine if fry survival differed between offspring of adults born in the wild and offspring of adults born in a hatchery. Equal proportions of fry from each group were stocked into the same reaches of natural streams and recaptured 3 months after stocking. Parentage analysis allowed each age-0 steelhead to be assigned to its group of origin, and we determined if the relative abundance of each group at capture equaled the relative abundance at stocking.

### Types of adult steelhead monitored

We monitored the survival of offspring from three groups of adult steelhead, which we refer to in this paper as NS for naturally spawning and $H_1$ and $H_2$ for one and two generations of artificial spawning in the hatchery. Adults that were born in the wild and spawned naturally in the wild are referred to as NS adults. Their offspring, which we monitored as age-1 and age-2 emigrating juveniles, are referred to as NS offspring. Adults that were born in the wild but captured at the Knife River adult trap and taken to French River Hatchery for artificial mating are labeled as $H_1$ adults. Their $H_1$ offspring were stocked as fry into upstream reaches of the Knife River and then monitored as age-1 and age-2 emigrants. The final group is the $H_2$ adults that were born in the hatchery and then stocked as age 1 with a fin clip. These fish matured in the wild but were not allowed to spawn naturally in the stream. They were captured at the Knife River adult trap, identified by their fin clip, and taken back to the hatchery for artificial mating. Their $H_2$ offspring were also stocked as fry into the Knife River and monitored as age-1 and age-2 emigrants.

### Rearing conditions

Rearing conditions were the same for both $H_1$ and $H_2$ offspring. In the French River Hatchery, eggs are loaded into trays at a constant density of 1500 eggs per tray. Trays are randomly placed on egg stands, and temperatures and dissolved oxygen levels between stands are nearly identical (M. Gottwald, MNDNR, 5351 North Shore Drive, Duluth, MN 55804, USA, personal communication, 2006).

### Fry stocking

In 2002, only $H_2$ fry were stocked into the Knife River. These fry were produced from 20 females, and matings were mostly one male crossed with one female but were not recorded. In 2003, adult steelhead were strictly mated one to one, all pairs were recorded, and both $H_1$ and $H_2$ offspring were stocked as fry (Table 1). Fry were stocked shortly after hatching at the time of yolk sac absorption. In the fall of 2003, 4841 $H_1$ fingerlings were stocked into the Knife River. This stocking was done independently of our study, and as a result, we could not distinguish survivors from fry versus fingerling stocking. This prevented us from making unbiased survival comparisons between $H_1$ and $H_2$ offspring from the 2003 year class in the Knife River.

Determining if family sizes were equal between all adult types required an accurate estimate of the number of NS females spawning in the Knife River in both 2002 and 2003. A single-census Peterson estimate was made to determine the number of females spawning upstream. All females captured in the trap on their upstream migration were marked with a floy tag, and those captured moving downstream were carefully examined for tags or evidence of a lost tag (tag stub or tagging scar). In 2002, 79 fish were marked on their way upstream, and 70 were captured on their way downstream, 53 of which were recaptures. Only one fish was found with a scar from a lost tag and was considered a recaptured fish. We thus estimated 104 NS females spawning upstream, with a 95% confidence interval (CI) estimated from the binomial distribution of 93–125 females. In 2003, 144 fish were marked on their way upstream, and 99 were captured on their way downstream, 80 of which were recaptures. Four fish were observed to have either a tag stub or tag scar, and these were considered recaptures. We thus estimated 178 NS

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**Table 1.** Juvenile steelhead stocked into the Knife River during the two study years from parents with one ($H_1$) or two ($H_2$) generations of artificial spawning in the hatchery.

| Year class | Type | Life stage | Number |
|---|---|---|---|
| 2002 | $H_2$ | Fry | 49 500 |
| 2003 | $H_1$ | Fry | 24 676 |
| | $H_2$ | Fry | 31 918 |
| | $H_1$ | Fingerling (fall) | 4 841 |

**Note:** Combined number of 29 517 $H_1$ offspring (fry + fingerling) used in statistical calculations of stocking success for 2003.

females spawning upstream with a 95% CI estimated from the binomial distribution of 164–203 females.

In 2003, only a portion of the offspring of $H_1$ parents was stocked as fry for this study; the rest were kept to continue the age-1 clipped juvenile stocking program. Families were pooled as eggs, so all families could have been sampled but exact family representation was unknown. The number of offspring stocked equaled 42% of the total fry produced by the 33 females spawned at the hatchery. We thus estimated that the equivalent of 14 females would have been required to produce the amount of fry stocked and used this value in calculations of juveniles per $H_1$ female.

### Juvenile steelhead

Fry were stocked into the Knife River in June of each study year and spent either one or two winters in the stream alongside the naturally produced fish before migrating to Lake Superior. Juvenile steelhead were captured in the Knife River juvenile trap between April and August in 2003–2005. In 2003 and 2004, scale samples for genetic analysis were taken from fish collected according to the routine MNDNR sampling protocol. Samples were taken from five unclipped fish per 10 mm size class per 2-week sampling period. This subsampling scheme was used to collect both age-1 and age-2 fish from the 2002 year class, but only age-1 fish from the 2003 year class. To obtain a larger sample size of age-2 juveniles from the 2003 year class, we collected scales from nearly all age-2 fish captured in the juvenile trap in 2005.

Age-1 steelhead, although often the largest emigrating group based on numbers alone, experience high mortality in Lake Superior, which limits their contribution to future adult returns. In our study, age-1 fish were examined to determine if the proportion of hatchery fish among age-1 emigrants equaled their proportion among age-2 migrants. A difference might indicate that hatchery ancestry affected age of emigration, which could contribute to observed differences in the number of age-2 juveniles produced.

### Paired stocking

Equal numbers of $H_1$ and $H_2$ fry were stocked into two streams in each of three years to determine if one type had a survival advantage. Adult steelhead of both types were captured at the Knife River trap during 2003–2005 and spawned at the hatchery. In 2003, 7485 fry of each type were stocked into Little Knife River and 6655 fry of each type were stocked into McCarthy Creek. In 2004, 7500 fry of each type were stocked into Stewart River and Budd Creek. In 2005, 7510 fry of each type were stocked into Stewart River and the West Branch Split Rock River (Fig. 1). Fry were stocked in June of each study year and were captured at age 0 by backpack electrofishing three months after stocking. Each captured juvenile fish had a portion of its caudal fin removed, which was stored in 95% ethanol for genetic analysis.

### Genetic and parentage analysis

We extracted DNA from all collected scale and fin samples with 250 µL of 5% Chelex® (Sigma Chemical, St. Louis, Missouri) solution and stored the samples at –20 °C following the protocol of Miller and Kapuscinski (1996). Polymerase chain reactions (PCR) were performed to amplify 11 microsatellite loci (Table 2). Reaction volumes were 15 µL and contained 6 µL DNA template, 10× polymerase buffer (10 mmol·L$^{-1}$ Tris–HCl, 50 mmol·L$^{-1}$ KCL, 0.1% Triton® X-100), 1.5 mmol·L$^{-1}$ $MgCl_2$, 0.2 mmol·L$^{-1}$ each dNTP, 0.5 µmol·L$^{-1}$ of each primer, 0.5 U Taq DNA polymerase (Promega, Madison, Wisconsin), and water up to the final reaction volume. Each plate included a water control to monitor for PCR contamination.

Thermal cycling conditions included 35 cycles of denaturation at 95 °C, annealing at 53 °C, and extension at 72 °C. We submitted PCR products to the Advanced Genetic Analysis Center (University of Minnesota, St. Paul, Minnesota) for electrophoresis on an ABI Prism 3100 genetic analyzer (Applied Biosystems, Foster City, California). Alleles were scored using the Applied Biosystems software program GENOTYPER.

We used the computer program WhichParents (W. Eichert, Bodega Marine Laboratory, University of California Davis, www.bml.ucdavis.edu), which uses an exclusion approach to parentage, to assign juvenile steelhead sampled at the Knife River trap to either a $H_1$ or $H_2$ parent pair. If a juvenile genotype was not compatible with any parent pair, it was considered to be produced by NS parents. Some juveniles from the paired-stocking experiment did not match any parents. In each of these cases, the stocking site was accessible by other fish and these mismatching individuals were removed from the analysis.

To ensure that our microsatellite set would not falsely assign a naturally produced juvenile to our set of hatchery parents, we created simulated populations of offspring to mimic what could have been produced in the wild. We used the software Whichloci (W. Eichert, Bodega Marine Laboratory, University of California Davis, www.bml.ucdavis.edu) to generate populations of 10 000 individuals based on the allele frequencies of each of the parent data sets. We then used the program WhichParents to determine if the simulated offspring genotypes matched any of our known parent pairs.

### Statistical analysis

We used $\chi^2$ analysis to test the null hypothesis of equal family size between the NS and $H_1$ or $H_2$ adults, using Yates correction for tests with one degree of freedom (Zar 1985). Specifically, we tested if the proportion of types among the emigrating juveniles equaled the proportion of types among the adult females that produced them. We considered age-1 and age-2 offspring separately. In 2002 we compared NS females with $H_2$ females, and in 2003 we compared NS with $H_1$ and NS with $H_2$. Family size ratios of one type to another

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**Table 2.** Diversity information of microsatellite loci used in parentage analysis, including name of each locus, number of alleles present, observed ($H_o$) and expected ($H_e$) heterozygosities, and frequency of null alleles in the parent generations.

| Locus name | Source | No. of alleles | $H_o$ | $H_e$ | Null allele frequency |
|---|---|---|---|---|---|
| *OGO3* | Olsen et al. 1998 | 10 | 0.77 | 0.66 | 0.00 |
| *OGO4* | Olsen et al. 1998 | 7 | 0.76 | 0.73 | 0.00 |
| *OKE4* | GenBank AF330221 | 17 | 0.91 | 0.91 | 0.00 |
| *OKI23** | GenBank AF272822 | 20 | 0.76 | 0.93 | 0.08 |
| *OMY1001* | Spies et al. 2005 | 19 | 0.84 | 0.89 | 0.00 |
| *OMY1011* | Spies et al. 2005 | 15 | 0.96 | 0.89 | 0.00 |
| *ONE108** | Olsen et al. 2000 | 26 | 0.81 | 0.90 | 0.05 |
| *ONE2* | Scribner et al. 1996 | 27 | 0.91 | 0.92 | 0.00 |
| *OTS4** | Banks et al. 1999 | 7 | 0.56 | 0.62 | 0.00 |
| *OTSB5** | Naish and Park 2002 | 15 | 0.77 | 0.86 | 0.03 |
| *RT191* | Spies et al. 2005 | 24 | 0.88 | 0.93 | 0.00 |

*Significantly different from Hardy–Weinberg expectations after sequential Bonferroni correction ($\alpha = 0.05$, $k = 11$).

were calculated by dividing the number of juveniles produced per female of the larger group by the number of juveniles per female of the smaller group.

Chi-squared tests were also used to analyze the results of our paired-stocking experiments. We tested if the relative abundance of juveniles of each group at capture equaled their relative abundance at the time of stocking. A 6 × 2 contingency table was used to determine if a significant difference existed between any of the years and streams used in the study.

Because female size may affect egg quality and, thus, early-life survival, we tested for a significant difference in the mean length and weight of adult females taken to the hatchery using two-sample *t* tests. We compared the size of $H_1$ and $H_2$ females during 2003, 2004, and 2005.

### Genetic composition of hatchery fish

To determine if the offspring produced in the hatchery accurately represented the genetic variation of the offspring produced naturally, we tested for population differentiation and differences in genetic diversity between the groups of hatchery and natural age-2 offspring in both the 2002 and 2003 year classes. We also tested the effect of differentiation on the genetic variation of the entire cohort following stocking. For each year class, we combined all age-2 offspring to estimate the allele frequencies of the entire cohort and compared them with the frequencies of only the NS fish. Difference in this comparison would represent a shift in allele frequencies of the entire cohort due to hatchery supplementation. Pairwise population differentiation tests were performed using FSTAT (version 2.9.3; Goudet 2001) to estimate $F_{st}$ and conduct permutations to test its significance and Genepop (Raymond and Rousset 1995) to perform exact tests for population differentiation. Expected heterozygosities and allelic richness by locus were also estimated using FSTAT. Because increasing sample size is expected to increase the number of alleles found, we used the FSTAT application that performs a resampling routine to estimate the number of alleles expected to be found with common sample sizes. Wilcoxon signed-rank tests (Zar 1985) were then used to test for differences in heterozygosity and allelic richness between sample groups.

## Results

### Parentage analysis

Simulation results demonstrated that we were unlikely to falsely assign naturally produced juveniles to either of our hatchery groups. In the simulated population based on allele frequencies of the 2002 parents, none of the 10 000 offspring uniquely assigned at all loci to a hatchery parent pair, neither did any match a parent pair at 10 of the 11 loci examined. Less than 1% matched both a male and female parent at nine of the 11 loci. The second simulated population based on the 2003 parents yielded similar results. No individual matched hatchery parents at nine or more loci. Approximately 1% of the 10 000 simulated offspring matched the parents at eight loci. The difference in the number of loci required to uniquely assign offspring between year classes is due to documentation of the hatchery mating scheme. In 2002, we did not have records of mated pairs, making it necessary to consider all possible crosses of males and females for parentage assignment. In all other years, the mated pairs were recorded in the hatchery, thus limiting the number of possible crosses in parentage analysis. In addition to the simulation results, no offspring from the paired-stocking experiments were assigned to more than one possible parent pair.

We were able to confirm null alleles present in three of the loci used in this study. While assigning parents to juveniles captured in Budd Creek, a 2004 paired-stocking site, we found some juveniles that matched known parents at only 10 of 11 loci. Given the isolated location of this stream and the results of our power analysis, it seemed improbable that these fish were from another source yet only mismatched our parents at one locus. Upon further inspection we found that each mismatch could be explained by the presence of a null allele in a parent that was passed on to the offspring. Of all juveniles sampled in these experiments, we did not observe an offspring with a null allele at all three of these loci. Only five individuals (of 730 uniquely assigned to a parent pair) with nulls at two loci were found, and they were included in the analysis because of the results of our power tests. The frequency of null alleles at each locus was estimated for the hatchery parent samples based on the con-

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**Table 3.** Number of juvenile emigrants from different parent types of Knife River steelhead, naturally spawning females (NS) and hatchery females with one ($H_1$) or two ($H_2$) generations of artificial spawning.

| | | Age 1 | | Age 2 | |
|---|---|---|---|---|---|
| Type | No. of females | No. of offspring | Offspring per female | No. of offspring | Offspring per female |
| **2002 year class** | | | | | |
| NS* | 104 | 47 | 0.45 | 63 | 0.61 |
| $H_2$ | 20 | 37 | 1.85 | 75 | 3.75 |
| **2003 year class** | | | | | |
| NS* | 178 | 167 | 0.94 | 806 | 4.53 |
| $H_1$* | 14 | 32 | 2.29 | 132 | 9.42 |
| $H_2$ | 19 | 26 | 1.37 | 110 | 5.79 |

**Note:** Types for which the numbers of females were estimates rather than direct counts are indicated with asterisks (*); see Methods for description. The number of offspring per female is low because of juvenile subsampling for all groups except the age-2 juveniles from the 2003 year class.

**Table 4.** Comparisons of steelhead family size, measured as age-1 and age-2 juveniles, between naturally spawning females (NS) and hatchery females with one ($H_1$) or two ($H_2$) generations of artificial spawning.

| | | Age 1 | | Age 2 | |
|---|---|---|---|---|---|
| Year class | Type comparison | $\chi^2$ value | Family size ratio | $\chi^2$ value | Family size ratio |
| 2002 | $H_2$:NS | 46.36** | 4.2 | 146.20** | 6.2 |
| 2003 | $H_1$:NS | 21.01** | 2.4 | 63.68** | 2.1 |
| | $H_2$:NS | 3.97* | 1.5 | 5.81* | 1.3 |

**Note:** $\chi^2$ tests (1 df) indicate if the proportion of types among the emigrating juveniles equaled the proportion of types among the adult females that produced them, with significant differences denoted by asterisks: *, $P < 0.05$; **, $P < 0.001$. Family size ratio is the number of offspring per female of the first type listed relative to the number per female of the second type, based on estimated female numbers.

firmed null alleles from parentage testing and ranged from 0.03 to 0.08 (Table 2). The presence of null alleles likely explains the Hardy–Weinberg disequilibrium at these three loci; of the remaining eight loci, only one was out of Hardy–Weinberg equilibrium after correction for multiple comparisons (Rice 1989).

### Fry stocking success

Fry stocking successfully increased the average family size of female steelhead. From the 2002 year class, $H_2$ females produced significantly more age-1 and age-2 offspring than did NS females. These hatchery adults produced 4.2 times more age-1 juveniles per female than did naturally spawning females and 6.2 times more age-2 juveniles (Tables 3 and 4). These results remained highly significant, even if the lower bound of the 95% CI for the number of NS females was substituted for the population estimate (age 1 $\chi^2 = 38.25$, 1 df, $P < 0.001$; age 2 $\chi^2 = 124.74$, 1 df, $P < 0.001$). A similar trend was observed from the 2003 year class. Both $H_1$ and $H_2$ females had significantly higher family sizes of both age-1 and age-2 offspring than did naturally spawning fish, although the family size ratio for each of the hatchery groups compared with the naturally spawning females was lower in the 2003 year class than it was in the 2002 year class (Table 4). The results for age-1 and age-2 $H_1$ steelhead remained highly significant if the lower bound of the CI was substituted for the population estimate (age 1 $\chi^2 = 25.00$, 1 df, $P < 0.001$; age 2 $\chi^2 = 101.80$, 1 df, $P < 0.001$); however, the difference between $H_2$ and NS steelhead was no longer significant (age 1 $\chi^2 = 2.64$, 1 df, $P = 0.104$; age 2 $\chi^2 = 2.59$, 1 df, $P = 0.108$).

### Paired-stocking survival comparisons

Paired-stocking comparisons showed an early life survival advantage for $H_1$ offspring over $H_2$ offspring when stocked at equal numbers into the same environment. In five of the six individual paired-stocking experiments, the number of $H_1$ juveniles captured exceeded the number of $H_2$ juveniles (Table 5); however, the difference in each was not significant owing to the low abundance of both groups at capture. A contingency table showed that there was no year or stream effect ($\chi^2 = 2.78$, 5 df, $P = 0.734$). All streams and years were then combined to achieve a larger sample size. In the resulting comparison, we found that significantly more $H_1$ juveniles were captured ($\chi^2 = 9.51$, 1 df, $P = 0.002$). The relative survival of $H_2$ to $H_1$ fish 3 months after stocking was 70%.

### Adult female size

We found a significant difference between the body size of $H_1$ and $H_2$ females in 2003. From the 2003 spawning class, 28 of the 33 $H_1$ females taken to the hatchery successfully produced at least one age-1 or age-2 juvenile. Fifteen out of 19 $H_2$ females produced offspring during the same spawning season. The successful $H_1$ females were significantly longer and heavier than the $H_2$ females (Table 6). In 2004 and 2005, there were no significant differences in length or weight between the groups.

### Genetic composition of hatchery fish

The offspring produced at the hatchery were genetically differentiated from those of naturally produced fish and had lower allelic richness. Pairwise $F_{st}$ was significantly greater

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**Table 5.** Numbers of age-0 steelhead with parents that had one ($H_1$) or two ($H_2$) generations of artificial spawning captured during three years of paired-stocking experiments in which equal numbers of each type were stocked as fry.

| Location | Year | Type | Number captured | $\chi^2$ (p value) |
|---|---|---|---|---|
| Little Knife River | 2003 | $H_1$ | 39 | 1.83 (0.175) |
| | | $H_2$ | 27 | |
| McCarthy Creek | 2003 | $H_1$ | 22 | 0.00 (1.000) |
| | | $H_2$ | 23 | |
| Stewart River | 2004 | $H_1$ | 45 | 1.55 (0.213) |
| | | $H_2$ | 33 | |
| Budd Creek | 2004 | $H_1$ | 24 | 2.13 (0.144) |
| | | $H_2$ | 14 | |
| Stewart River | 2005 | $H_1$ | 13 | 1.25 (0.260) |
| | | $H_2$ | 7 | |
| West Branch Split Rock River | 2005 | $H_1$ | 44 | 3.61 (0.057) |
| | | $H_2$ | 27 | |
| All streams and years combined | 2003–2005 | $H_1$ | 187 | 9.51 (0.002) |
| | | $H_2$ | 131 | |

**Note:** $\chi^2$ tests showed whether relative abundance of each type at capture equaled relative abundance at stocking, for each year and site separately and for all data combined.

**Table 6.** Results of two-sample *t* tests for difference in size between hatchery females with one ($H_1$) or two ($H_2$) generations of artificial spawning.

| Year | Type | Number sampled | Mean weight (kg) | *t* (*p* value) | Mean length (mm) | *t* (*p* value) |
|---|---|---|---|---|---|---|
| 2003 | $H_1$ | 28 | 2.4 | 4.43 (<0.001) | 627 | 3.69 (<0.001) |
| | $H_2$ | 15 | 1.7 | | 554 | |
| 2004 | $H_1$ | 7 | 2.8 | 0.26 (0.800) | 655 | 0.62 (0.541) |
| | $H_2$ | 12 | 2.7 | | 643 | |
| 2005 | $H_1$ | 7 | 2.5 | −1.09 (0.298) | 660 | −0.27 (0.789) |
| | $H_2$ | 6 | 2.8 | | 668 | |

**Table 7.** Comparisons of expected heterozygosity ($H_e$), allelic richness ($A$), and population differentiation ($F_{st}$) for samples of age-2 steelhead with parents that had one ($H_1$) or two ($H_2$) generations of artificial spawning or were spawned naturally (NS).

| Year class and group | Sample size | $H_e$ | $A$ | Pairwise $F_{st}$ | |
|---|---|---|---|---|---|
| | | | | $H_2$ | NS |
| 2003 | | | | | |
| $H_1$ | 132 | 0.84 | 13.8 | 0.03* | 0.01* |
| $H_2$ | 110 | 0.83 | 12.0*** | — | 0.02* |
| NS | 806 | 0.83 | 14.8 | 0.01* | — |
| Cohort | | — | — | — | 0.00 |
| 2002 | | | | | |
| $H_2$ | 75 | 0.78 | 9.6** | — | 0.05* |
| NS | 63 | 0.83 | 13.9 | 0.05* | — |
| Cohort | | — | — | — | 0.01* |

**Note:** Means are shown for $H_e$ and $A$, but testing was based on the Wilcoxon signed-rank test. Significance for pairwise $F_{st}$ tests (i.e., $F_{st} > 0$) was based on permutations tests. Significant results are indicated with asterisks: *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$. The cohort category grouped all H and NS together and compared them with NS alone.

than zero in all comparisons between H and NS offspring for both year classes (probability was <0.05 that $F_{st} = 0$ following permutation tests in FSTAT; Table 7). The entire 2002 emigrating cohort (NS and $H_2$) was also significantly differentiated from the 2002 NS fish alone; however, the 2003 emigrating cohort (NS, $H_1$, and $H_2$) did not differ significantly from the 2003 NS fish. Exact tests for population differentiation performed in Genepop produced the same significant comparisons (data not shown). Expected heterozygosities did not differ between H and NS offspring in any comparisons (all $P \geq 0.10$, Wilcoxon signed-rank tests, $n = 11$). In contrast, allelic richness was significantly lower for $H_2$ offspring compared with NS offspring for both year classes and lower, but not significantly, for $H_1$ offspring in 2003 ($P = 0.18$, Wilcoxon signed-rank test, $n = 11$).

## Discussion

We have shown that a steelhead fry stocking program was successful as measured by an increased number of offspring produced by hatchery females relative to naturally spawning females. By circumventing the perils of spawning and incubation in the wild (egg-to-fry survival was approximately 70% in the hatchery), hatchery rearing produced large numbers of fry per female, ultimately leading to increased numbers of age-2 offspring. This measure of stocking success is necessary, but not sufficient, to achieve a goal of population rehabilitation. To achieve a self-sustaining increase in population abundance, the stocked fish must add to the population rather than displace naturally produced offspring, and

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short-term increases in abundance must not be negated by fitness impacts of hatchery fish on wild populations. We found reduced survival of offspring of parents with only one generation of hatchery ancestry. This indicates that the fitness impacts of domestication selection (Reisenbichler and McIntyre 1977; Fleming et al. 1997; Dannewitz et al. 2003) can occur in the early generations of a hatchery program.

In both years of our study, we observed that fry stocking successfully increased the number of emigrating juveniles produced per spawning female. Steelhead that emigrate to Lake Superior as age-2 juveniles are more likely than age-1 emigrants to return as spawning adults (Schreiner 2003) and are thus of most importance to managers. We found that a female steelhead spawned in the hatchery was able to produce more age-2 offspring than a steelhead spawning naturally. The success of stocking $H_1$ fry in 2003 may have been inflated by the late fall stocking of fingerlings, which we grouped with fry in our analyses; however, the $H_2$ females, which had only fry stocked, also produced more offspring than natural spawners, and the greater success of $H_1$ over $H_2$ was consistent with the results of our paired-stocking experiments. We also observed no significant difference in the proportion of emigrants, derived from stocked fry, that left the river as age 1 or age 2. This indicates that stocked fry did not differ from natural fry in their age at emigration, a critical factor in determining likelihood of survival to adulthood.

We could not directly measure whether the fry stocked in this study merely displaced some naturally reproduced juveniles or actually added to them; however, a negative correlation between adult abundance and success of fry stocking between study years was consistent with additions to the population. In 2002 we estimated that there were 104 female steelhead spawning in the Knife River and the $H_2$–NS family size ratio for that year class at age 2 was 6.2:1. In 2003 the number of females increased to 178, whereas the ratio of the groups spawned in the hatchery to naturally produced fish dropped to 2.1:1 and 1.3:1 for $H_1$ and $H_2$ females, respectively. The offspring of these extra females in 2003 would have used more habitat in the river, leaving less available for the stocked fry. Our results suggest that the fry stocking did add to the population, at least in one year, but it will cease to be productive when the carrying capacity of the river is met. Careful monitoring of stocking success and correlating the number of age-2 juveniles produced with the number of adults spawning and the environmental conditions will allow for determination of when stocking is no longer productive.

The paired-stocking study allowed us to directly compare the survival of fry from $H_1$ and $H_2$ parents. The relative survival of $H_2$ to $H_1$ was 70% after 3 months of in-stream life. We found no significant difference between streams or years; however, if we removed 2003 from the analysis, owing to the possible influence of female size, there was still a significant advantage for $H_1$ offspring. Using only 2004 and 2005 paired-stocking data, the relative survival of $H_2$ to $H_1$ actually dropped to 64%. In addition, the relative survival of $H_2$ to $H_1$ was 75% among the age-2 emigrants from the 2003 year class stocked in the Knife River (data not shown), although this comparison was confounded by the additional stocking of $H_1$ fingerlings. Araki et al. (2007*a*) found similar effects of hatchery ancestry on reproductive success of local-origin first-generation hatchery steelhead. Hatchery female × hatchery male crosses had 66% reproductive success relative to wild female × hatchery male crosses (Araki et al. 2007*a*; Table 5). When keeping the female constant, hatchery male × hatchery female crosses had 90% reproductive success relative to wild male × hatchery female crosses, although this result was not significant. Araki et al. (2007*b*) extended this study to additional run years and a second generation and found significant reductions in reproductive success of hatchery fish relative to wild fish over the first two generations. Their meta-analysis of relative reproductive success of local captive-reared versus wild fish suggested a decline of 37.5% per generation.

The observed difference in survival between the two groups of fry stocked in our study was likely due to lesser exposure of $H_1$ to domestication selection than $H_2$. The fry groups experienced the same rearing environment, suggesting a genetic component to the survival differences. The only life history difference between parents of $H_1$ and $H_2$ offspring was the place of birth and rearing during their first year of life and the additional generation of artificial mating. The year of relaxed natural selection, experienced by the $H_2$ adults in the hatchery, undoubtedly enabled some of them to survive that otherwise may not have. When offspring of those parents had to compete in the wild with fish that had no hatchery history, they were less able to do so and experienced reduced survival. Our finding is consistent with the conclusion by Reisenbichler and Rubin (1999) that rearing fish for one year or longer in a hatchery causes genetic change and decreases both their fitness and that of their offspring.

We could not explicitly test for maternal effects, but we did examine one potential contributing factor, female size. In 2003, $H_1$ females were significantly larger than $H_2$ females, which in other studies has been shown to increase the survival chances of offspring (e.g., Pitman 1979; Kinnison et al. 1998; Einum and Fleming 2000). Of all six paired-stocking comparisons over 2003–2005, the only one that did not favor $H_1$ was McCarthy Creek in 2003. At all sites in 2004 and 2005, $H_1$ was favored over $H_2$ in spite of no size difference for the females in these years. Other maternal effects could have been present but were likely negligible because the females shared a common stream and lake environment for the majority of their lives (i.e., after the stocking of $H_2$ at age 1).

The hatchery practices used during this fry stocking program shifted allele frequencies enough to segment the Knife River steelhead population into distinct groups; however, the long-term effect of this segmentation depends on the success of the stocking (Ryman and Laikre 1991; Waples and Do 1994). The use of a relatively small number of adults at the hatchery led to genetic differentiation between stocked fry and the naturally produced fish. This was caused by a change in allele frequencies and the loss of some alleles. In 2002, the high success of $H_2$ fry overwhelmed the naturally produced fish, and the cohort as a whole experienced a shift in allele frequencies from the natural population. In 2003, the success of the stocked fry was not as great, and a larger number of naturally produced fish prevented the stocked fry from significantly changing the allele frequencies of the entire cohort. Even if some cohorts experienced shifts, returning different adults to the hatchery in consecutive years may eventually capture more of the genetic variation within the population. For example, Heggenes et al. (2006) documented

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no significant shift in genetic diversity from 20 years of supplemental steelhead stocking in British Columbia; however, they did show that some rare alleles were lost in the population. Careful monitoring of Knife River steelhead will be required to determine what effects hatchery practices may have on the genetic variation of the population in the long term.

Reproductive success should be measured throughout an entire life cycle, but the fry that were stocked have not recruited to spawning age in sufficient numbers for evaluation. Those data would represent the most complete measure of fry stocking success and would provide the most conclusive results about the effects of one generation of hatchery experience upon fitness of offspring. Our preliminary conclusion of stocking success could be tempered if hatchery juveniles have reduced survival as they mature into adults. However, even without the rate of adult returns, our study demonstrates the reduced survival of offspring of parents that spent their first year of life in a hatchery.

The goal of steelhead management in the Knife River is to reestablish a population large enough to allow limited angler harvest, supported mainly by natural reproduction (Schreiner 2003). The MNDNR has eliminated harvest of natural steelhead and promotes appropriate land use to maintain or increase available habitat. We have shown that fry stocking increased the reproductive success of hatchery females and may also contribute to achieving the management goal; however, cautions do exist. Our data suggest that domestication selection may be reducing survival of fry after only one generation of hatchery experience. Domestication selection is not understood well enough to predict its effects on future generations or how quickly it can be counteracted by natural selection, but modeling has shown that its long-term impacts can be significant (Ford 2002). Additionally, genetic change as a result of enhancing only a small portion of the population is occurring with current practices, at least within some cohorts. Steps must be taken to ensure that sufficient genetic variability remains in the population. These risks must be weighed against the benefits of fry stocking, and a recovery method that provides an immediate boost in population size yet reduces genetic risks should be developed (Miller and Kapuscinski 2003). Any management strategy must be met with a commitment to future monitoring and evaluation of this population and the hatchery practices associated with it.

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# Predictive modeling and spatial mapping of fish distributions in small streams of the Canadian Rocky Mountain foothills

**Richard J. McCleary and Marwan A. Hassan**

**Abstract:** We developed an automated procedure for modeling spatial distribution of fish occurrence using logistic regression models and geographic information system (GIS) tools. Predictors were measured from a digital elevation model (DEM) and stream layers. We evaluated the accuracy of GIS measures of reach slope through a comparison with field measures. Resource selection function models were used to explain presence–absence of bull trout (*Salvelinus confluentus*), rainbow trout, (*Oncorhynchus mykiss*), nonnative brook trout (*Salvelinus fontinalis*), and all fishes. Our models were extrapolated based on low, medium, and high levels of probability to produce reach-scale maps across 12 000 km$^2$. We attempted to improve models by adding land-use variables; however, the terrain best suited to road building and harvest also contained the habitat selected by rainbow trout, whereas bull trout generally selected terrain too steep for land use. These confounding factors emphasize the need for process-based investigations in addition to correlative approaches to identify habitat requirements. This automated method provides a rapid evaluation of fish habitat across remote areas useful for salmonid conservation and research planning.

**Résumé :** Nous avons mis au point une procédure automatisée pour modéliser la répartition spatiale de l'occurrence des poissons à l'aide de modèles de régression logistique et d'outils du système d'information géographique (GIS). Les valeurs prédictives ont été mesurées d'après un modèle digital d'altitude (DEM) et la couche des cours d'eau. Nous avons évalué la précision des mesures GIS des pentes des sections par comparaison avec des mesures de terrain. Des modèles de fonction de sélection des ressources ont servi à expliquer la présence–absence de l'ombre à tête plate (*Salvelinus confluentus*), de la truite arc-en-ciel (*Oncorhynchus mykiss*), de l'omble de fontaine (*Salvelinus fontinalis*) non indigène et de l'ensemble des poissons. Nous avons extrapolé nos modèles à des niveaux bas, moyens et élevés de probabilité pour produire des cartes à l'échelle des sections sur 12 000 km$^2$. Nous avons essayé d'améliorer les modèles en ajoutant des variables d'utilisation des terres; cependant, les surfaces les plus appropriées pour la construction de routes et pour les récoltes contiennent aussi les habitats sélectionnés par la truite arc-en-ciel, alors que l'ombre à tête plate choisit généralement des terrains trop escarpés pour utilisation humaine. Ces facteurs confondants soulignent la nécessité de faire des investigations reliées aux processus en plus d'utiliser les méthodes de corrélation pour identifier les besoins en habitats. Notre méthode automatisée fournit une évaluation rapide des habitats des poissons dans des régions éloignées qui est appropriée pour la conservation des salmonidés et elle permet une planification de la recherche.

[Traduit par la Rédaction]

## Introduction

Quantifying fish distributions in streams and extrapolating these occurrence patterns beyond sampled areas can provide knowledge to support fish conservation planning and guide detailed experimental investigations (Rosenfeld 2003). Impediments to extrapolation of occurrence patterns include identifying key parameters that can be accurately measured with remote methods and addressing scaling issues related to the hierarchical nature of stream systems.

Approaches to modeling fish distributions differ between regions and land-use types. Differences in terrain limit model transferability. Models of fish occurrence used in headwater streams of the mountainous regions of western North America include descriptors of stream size, reach slope, and disruptions in stream connectivity created by obstructions to fish migration (Fransen et al. 2006). Geomorphic characteristics that dictate thermal regime also influence habitat selection by salmonids (Baxter and Hauer 2000). Fish habitat and distribution in the Great Plains of

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central North America have been impacted by agriculture, reservoir construction, and urbanization, and as a result, models of fish distribution include a greater number of variables to describe environmental gradients and land use (Oakes et al. 2005).

Impacts to fish habitat from riparian logging are emphasized in some regions; however, these effects are not relevant in the Rocky Mountain foothills (foothills) where riparian buffer strips have been used since the onset of industrial forest harvest in 1956 (Bott et al. 2003). Likely impacts include sedimentation from logging roads (Spillios 1999), bank erosion, and habitat loss due to obstructions at culverts (Scrimgeour et al. 2003). However, relations between land use, habitat impacts, and fish occurrence have not been studied extensively in the continental rain and snow climate of the foothills.

Habitat studies have historically focused on large streams that provide water, power, and habitat for sport fish; less is known about small streams that represent most of the watercourses on the landscape (Moore and Richardson 2003). In comparison to large streams where fish presence can generally be inferred, only a portion of the small streams on the landscape provide habitat suitable for fish. In small streams, land use has a greater possibility of altering fish habitat features created by streamside vegetation and large woody debris (Hassan et al. 2005). Small streams can also be suitable for low-cost culverts at road crossings; however, where fish are present, these structures may obstruct fish passage (Wolter and Arlinghaus 2003). Fish presence at such locations should be ruled out by conducting electrofishing inventories during different years and seasons and by considering characteristics of the channel network. In the foothills, most small streams are inaccessible and located in a region of growing industrial activity. Environmental assessments for proposed projects ideally include electrofishing inventories. However, information on fish-bearing status may be required on short notice or outside of the summer season during which conditions are suitable for electrofishing. The sensitivities of small streams to a variety of land-use impacts and the increasing rate of industrial development warrants a remote-sensing approach to providing fish occurrence information.

The main objective of this research was to develop an automated method to predicting fish occurrence in small foothills streams. This knowledge is important to support planning of road locations and design of stream-crossing structures. Development of this approach is timely in Alberta because of the rapid expansion of the petroleum exploration and extraction industries. Fish occurrence information is also necessary when designing processed-based geomorphic and aquatic studies. The specific objectives of the research are (*i*) to map distributions for individual fish species and for all fishes regardless of species, (*ii*) to determine the most important variables for explaining occurrence, (*iii*) to compare distributions of native and nonnative fish, and (*iv*) to identify relationships between land use and occurrence of individual species.

We sought to address a number of common pitfalls when predicting distributions of organisms. First, the accuracy of variables measured with a geographic information system (GIS) is often not validated with field-measured data. Second, many researchers report a model's predictive accuracy; however, this measure is systematically affected by the frequency of occurrence of the target organism (Olden et al. 2002). Third, few models are validated with an independent data set (Olden et al. 2002). Fourth, it is difficult to design a sampling program to capture multiple environmental gradients when land-use variables are included. Land-use activities are not ubiquitous across the landscape (Van Sickle et al. 2004), rather their locations are based on criteria that may be similar to those of native fishes adapted to specific niches. In the foothills, harvesting has always been limited to terrain with less than 40% slope because of the limitations of logging equipment (Bott et al. 2003). Exclusionary distributions of land use and fish occurrence create a layer of complexity that confounds the interpretation of model outputs. Finding solutions to these four difficulties will advance the use of GIS-based resource selection function models.

## Materials and methods

### Study area

The study area covers a 12 000 km$^2$ portion of the foothills in west-central Alberta (Fig. 1). The foothills, underlain with sandstone and siltstone, represent a transition zone between the interior boreal plains to the east and the carbonate-dominated front ranges of the Rocky Mountains to the west. The combination of highly erodible bedrock and extensive glaciation has created a rolling topography. Elevations range from 1000 to 1600 m. Lodgepole pine (*Pinus contorta*) and white spruce (*Picea glauca*) forests cover uplands, and either black spruce (*Picea mariana*) – tamarack (*Larix laricina*) forests or shrubs dominate wet areas. Approximately 1% of the land base (120 km$^2$) is harvested annually, and the first harvest rotation will be completed by 2040.

### Fish species

This study focused on bull trout (*Salvelinus confluentus*), rainbow trout (*Oncorhynchus mykiss*), and introduced brook trout (*Salvelinus fontinalis*). Bull trout are designated as a species of special concern in Alberta. The Athabasca River watershed (Fig. 1) is one of three basins east of the continental divide that support native rainbow trout (Taylor et al. 2006). Both nonnative and native rainbow trout inhabit the study area, but small streams provide important habitat for genetically pure native populations (Taylor et al. 2006). Brook trout were first introduced in Alberta in 1922, and widespread introductions in the 1960s included headwater lakes in the Athabasca River watershed (Donald et al. 1980). Bull trout have a very high sensitivity to angling, road-related sediment, road-related migration barriers, and increases in water temperature (Rieman and McIntyre 1993), whereas rainbow trout have a high sensitivity (Ford et al. 1995*b*) and brook trout have a moderate to high sensitivity to these impacts (Ford et al. 1995*a*). Brook trout present a threat to the long-term conservation of bull trout through hybridization (Leary et al. 1993) and juvenile competition (Selong et al. 2001). Knowledge of spatial distributions of these native and nonnative fishes may assist conservation efforts.

We used fish occurrence data from three different projects (Fig. 1): we collected information within the monitoring watersheds (MW) specifically for this study and obtained

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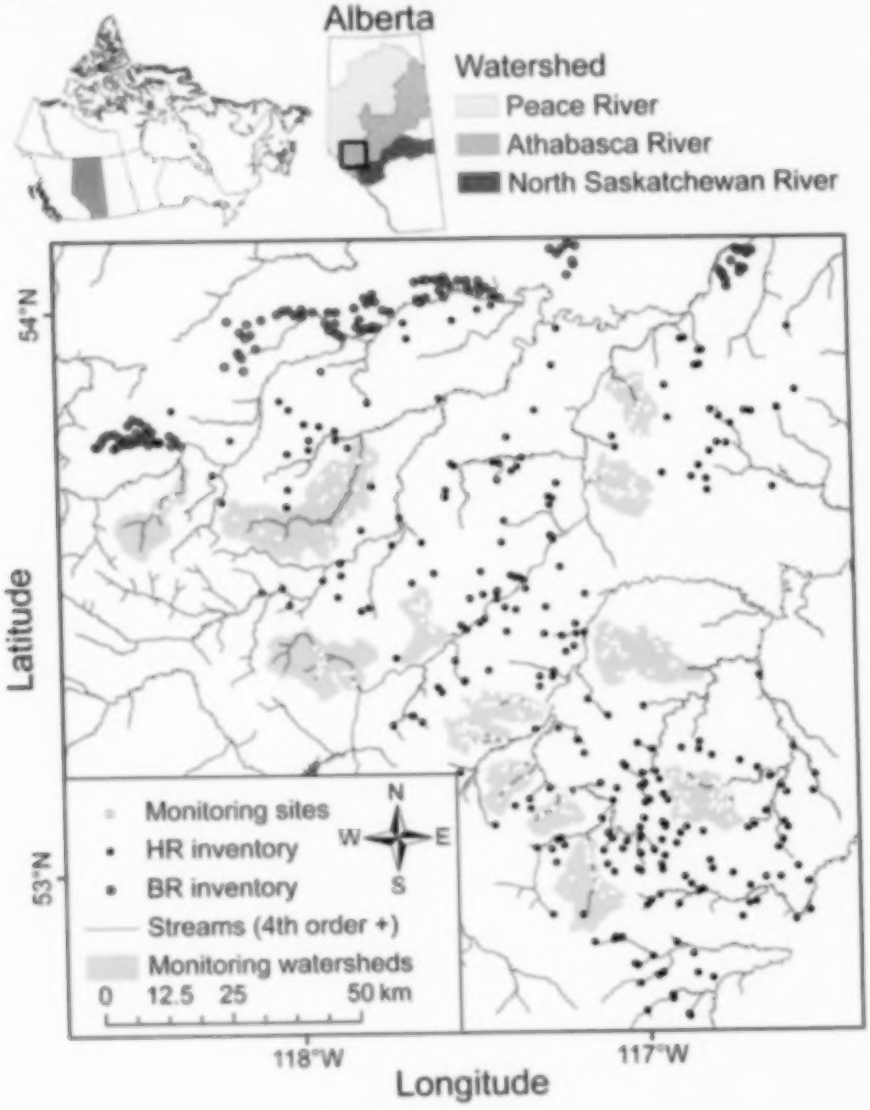
**Fig. 1.** Map of the fish sampling locations by project, including monitoring watersheds (model training data set), Hinton region (HR) inventory (model testing data set), and Berland region (BR) inventory (model testing data set).




data from Hinton region (HR) and Berland River region (BR) inventories for the purposes of model validation. In the HR inventory, forest planners selected sites where fish presence–absence information was required to conserve fish passage at existing and proposed road–stream crossings. The BR inventory, completed in 1995 and 1997, was a reconnaissance survey of a largely pristine area scheduled for forest harvest.

The study area includes the subalpine, upper foothill, and lower foothill natural subregions (Beckingham et al. 1996). For detailed analysis, we selected 15 watersheds representing the range of biophysical and land-use characteristics for the study area (Fig. 1). For the MW and HR inventories, technicians used a backpack electrofisher (model 12A; Smith-Root Inc., Vancouver, Wash.) to sample 300 m long reaches. For the BR inventory, a Coffelt Mark 10 (Coffelt Manufacturing, Inc., Flagstaff, Arizona) was used, and reaches in first- and second-order streams were reduced to 150 m. Electrofishing was deferred when elevated flow or turbidity levels could have affected capture. A single-pass survey with no block nets was used to determine fish presence–absence. We randomly selected sample sites from the various stream-order and stream-slope combinations within each of the 15 monitoring watersheds, and these sites were sampled between 1999 and 2002. Additional fish presence–absence data within the 15 watersheds were obtained for a small number of sites that were monitored between 1996 and 2002.

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### An automated procedure to measure basin and reach characteristics

To map predicted probabilities of target fish species in the study area, we needed a system to extrapolate findings from specific sample points across the study area. This approach required a set of predictor variables that could be calculated through GIS analyses of existing data. An automated procedure to measure these variables included two stages. Before completing these stages, we prepared a single-line stream network and hydrologically corrected the digital elevation model (DEM) (Duhaime 2003).

In the first stage (reach-break creation), the stream network was divided into a series of distinct sections based on topologic (stream network) and topographic (slope) criteria. Reach breaks were placed at all confluences and topological features such as waterfalls and lake boundaries. We then used a two-step process for the creation of topologic breaks. In the first step, preliminary reach breaks were placed every 100 m in an upstream direction from each topologic reach break. In the second step, preliminary topologic reaches were amalgamated wherever the change in slope from a downstream segment to the next segment upstream failed to exceed a given tolerance. To achieve an average reach length of 300 m for all streams in the study area, the tolerances changed with downstream reach slope as follows: slope ≤ 1%, tolerance = 0.5%; 1% < slope ≤ 2%, tolerance = 1.0%; 2% < slope ≤ 4%, tolerance = 1.5%; 4% < slope ≤ 6%, tolerance = 2.0%; 6% < slope ≤ 10%, tolerance = 3.0%; 10% < slope ≤ 20%, tolerance = 5.0%; 20% < slope ≤ 40%, tolerance = 10%; slope ≤ 40%, tolerance = 20%. The process proceeded in an upstream direction from each stream confluence. Reach breaks were retained at topologic features and stream confluences.

The second stage consisted of the creation of watershed boundaries representing a drainage-area polygon originating at the downstream end of each reach. The polygons were created using a nested approach to ensure consistent boundaries between adjacent watersheds and to facilitate editing. The drainage-area boundary for each reach was saved to permit calculation of basin-scale variables for each reach.

### Accuracy of stream slope measures generated from a DEM

To evaluate the accuracy of measures of stream slope derived from a 25 m DEM, we measured true stream slope with a total station (Lecia model TPS700; Lecia Geosystems AG, St. Gallen, Switzerland) and prism pole at 23 stream reaches. Surveys extended for a distance equivalent to 50–100 channel widths and points were captured at all bed-feature and meander transitions. We found a meandering channel pattern in most reaches that extended into headwater positions. Stream banks were well vegetated and root structures promoted meander development. For each survey, line length was the sum of the horizontal distances between successive points. Straight-line distance was calculated using the start and end points. Using GIS (ArcMap Version 9.2; ESRI Corporation, Redlands, California), we isolated the mapped stream segments that corresponded to our field-surveyed reaches. Then we calculated the change in line length by dividing the total length of the mapped stream reach by the total length of the surveyed stream reach (McMaster 1986). Stream reaches with a drainage area greater than 20 km$^2$ had small changes in line length, indicating reasonable discernment of the channel pattern during aerial photograph interpretation. Below this threshold, the change in line length averaged 78%, indicating greater generalization and poor representation of channel meanders. After applying this channel length correction factor to all reaches with a drainage area < 20 km$^2$ (corrected slope = slope × 0.78), there was no longer any evidence of differences between field-surveyed slope and GIS slope for the corresponding segment (paired $t$ test, $P_{\text{before}} = 0.002$, $P_{\text{after}} = 0.954$) or between field-surveyed slope and GIS reach slope from the automated procedure ($P_{\text{before}} = 0.017$, $P_{\text{after}} = 0.645$).

### Deriving predictive models of fish occurrence

The strategy that we used to explore relationships between fish presence–absence and habitat descriptors has been used in related studies (e.g., Ripley et al. 2005) and is consistent with the information–theoretic approach to model development and selection. This approach differs from traditional hypothesis testing in three ways (Burnham and Anderson 2002). First, the researchers identify a set of candidate models from patterns described in the literature and their observations. Second, the best model is identified using the Akaike's information criterion that considers both parsimony and the fit of each candidate model to the phenomenon or process of interest. Third, this approach does not use hypothesis tests or $p$ values.

We calculated the small-sample version of Akaike's information criterion ($AIC_c$) and included a preliminary test for overdispersion (Burnham and Anderson 2002). Following the calculation of $AIC_c$, we estimated an evidence ratio ($\Delta_i$) and Akaike weights ($w_i$) to help select the most parsimonious model and further provide rankings of model importance and uncertainty. The model with the lowest $\Delta_i$ is the best-fit model out of the candidate set of models, and $w_i$ provides an approximate representation for the probability of a particular model fitting the data compared with the candidate set of models. To accomplish our objectives, two separate model-selection exercises were undertaken.

In the first exercise, the candidate models were limited to those containing predictor variables describing fish habitat at each stream reach. These variables, which we call ecological variables, represented key habitat dimensions including size, energy, and climate (Bozek and Hubert 1992) and were measured from readily available digital information sources. The best model developed from the ecological variables provided distribution information exclusive of land use and was well suited to extrapolation. The second set of models included combinations of the best ecological model and three land-use variables. The land-use variables were intended to represent management activities that could have affected the productive capacity of fish habitat in small streams.

We identified six ecological variables and three land-use variables (Table 1). All candidate ecological models included area because of its importance in most fish occurrence models (Rosenfeld 2003). The complete set of candidate ecological models included all combinations of area and noncorrelated variables. The set of candidate ecological – land-use models included the variables from the best ecolog-

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**Table 1.** Reach-scale variables grouped by category.

| Variable code | Predictor variable, measurement methods, and fish habitat considerations |
|---|---|
| **Ecological parameters** | |
| Area | Drainage area above downstream end of reach ($km^2$); common variable in fish occurrence modeling (Rosenfeld 2003) |
| Basin slope | Mean basin slope (%); calculated as the mean slope percentage from all DEM cells in the catchment of each reach; common variable in fish occurrence modeling; related to annual sediment yield in region (McPherson 1975) |
| Basin elevation | The average elevation (m) from all DEM cells in the catchment of each reach; ecosystem productivity decreases and annual precipitation increases with elevation within study area (Beckingham et al. 1996) |
| Percent wetlands | Percent of drainage area occupied by wetlands on forest inventory map; muskegs are common in region and typically form along lower side slopes and depressional areas (Dumanski et al. 1972); wetlands include black spruce (*Picea mariana*) – tamarack (*Larix laricina*) and shrub–herb communities; we observed low fish occurrence and organic substrate within streams that drain wetlands |
| Reach elevation | Elevation at downstream end of reach (m) |
| Reach slope | Common variable in fish occurrence modeling (Rosenfeld 2003) |
| **Land-use parameters** | |
| Harvest | Percent of basin harvested since 1956 measured from timber inventory maps; percent harvest was associated with a lower probability of bull trout occurrence within region (Ripley et al. 2005) |
| Road density | Length of permanent roads within each basin ($km \cdot km^{-2}$) measured on road maps; impact water quality and peak flow (MacDonald et al. 1990); related to decreased bull trout redd numbers (Baxter et al. 1999) |
| Downstream barrier | All reaches with a potential barrier located in downstream areas were coded yes (1) and others were coded no (0); culverts that retain an uninterrupted natural bottom conserve fish migration and all others may present a barrier depending on hang height, water velocity, fish species, and life stage (Jackson 2003); therefore, barriers included all culverts, except those with substrate retained within the culvert and without any hanging outfall; fish migration barriers at road crossings represent challenge for fish population conservation in some foothills streams of Alberta (Scrimgeour et al. 2003) |

**Note:** Ecological variables were measured at all reaches across the study area. Land-use variables were measured for all reaches within the monitoring watersheds. Bull trout, *Salvelinus confluentus*.

ical model with all combinations of the three land-use variables.

Before model development, colinearity between all continuous ecological and land-use variables was assessed using Pearson correlation tests. To avoid colinearity, we excluded one of the variables when correlations were greater than |0.6|. We used a data-splitting type of cross validation (Olden et al. 2002), with 80% of the MW samples randomly selected for model training and the rest used for model testing. A nonlinear quadratic relationship was expected for ecological variables because of the adaptation of most organisms to a specific niche. Before model development, we used a two-step process to identify such patterns. For each predictor variable, we determined the average percent occurrence across 10 evenly sized classes. Next, we plotted relations for percent occurrence by predictor variable class to identify nonlinear relations. When these patterns were apparent, we included a quadratic term within model structures (i.e., basin slope + basin slope$^2$). Logistic regression was used to compare fish species present sites (1) with absent sites (0) based on ecological covariates of interest and candidate models tested.

### Model interpretation and validation

Interpretation of regression coefficients was complicated by different measurement units among variables. To ensure that the value of regression coefficients corresponded to the magnitude of the effect on probability, all continuous predictors were scaled to standardized scores with mean value of 0 and variance of 1 (Klienbaum et al. 1988). Odds ratios (ratio of probability that event will occur to probability that it will not occur) and associated confidence intervals were also calculated. When a regression coefficient equals 0, its odds ratio equals 1. Therefore, when a confidence interval includes 1, it cannot be concluded that the variable is associated with a change in odds.

We assessed model performance based on receiver–operator characteristic (ROC) and cross-validation. For the best ecological models, we used four data sets (MW training and testing and HR and BR inventories). Land-use data were not available for the HR and BR inventories. The ROC evaluation included two components. First, we reported the area under the ROC curve where 0.5–0.7 represented low, 0.7–0.9 represented intermediate, and >0.9 represented high model accuracy (Manel et al. 2001). Second, we established high and medium probability cutoffs. Logistic regression is well suited to studies on rare organisms because the probability cutoff for establishing presence–absence varies with prevalence. The high probability cutoff corresponded to the point where the model sensitivity (probability of correctly predicting a positive outcome) and model specificity (probability of correctly predicting a negative outcome) were both maximized. We set the medium probability cutoff at one-half the value of the high probability cutoff. Probabilities less than the medium cutoff were assigned a low probability. Based on the high and medium cutoffs, we reported sensitivity (true positives correctly classified), specificity (true negatives correctly classified), and overall accuracy. The Canada

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Fisheries Act provides protection of all fish habitat, including stream reaches with infrequent use; therefore correct identification of positive outcomes (sensitivity) is more important than correct identification of negative outcomes (specificity). For the sensitivity evaluation at both cutoffs, low, medium, and high performances were represented by values <70, 70–90, and >90, respectively.

We included Cohen's kappa as a fourth validation statistic, because unlike sensitivity, specificity, and overall accuracy, it provides an assessment of correct predictions outside of chance expectations (Manel et al. 2001). Low, medium, and high model performances were represented by kappa values <0.4, 0.4–0.6, and 0.6–0.8, respectively.

### Extrapolating and mapping occurrence models

We used a simple procedure to extrapolate the best AIC models and produce distribution maps by species for the study area. First, we exported a table from the GIS with unique reach numbers and values for all ecological variables for the 40 000+ reaches within the study area. This table was appended to the table containing the model training data and the combined table was imported into the modeling program (SPSS version 10.0.5; SPSS Inc., Chicago, Illinois). We ran the best model for each species and used the function to save predicted probability values for each reach. The predicted probabilities for all reaches were linked back to the reach table in the GIS. Probability of occurrence was mapped using three categories (high, medium, and low) based on the ROC-determined cutoff value for each model.

### Sources of error

Errors in fish occurrence can result when the minimum number of fish present in a reach is less than the minimum detectable population for the capture technique. Paul and Post (2001) used similar capture techniques (single-pass electrofishing, 300 m reach, and no block nets) in the foothills and determined a minimum detectable density of 8 individuals·(300 m)$^{-1}$. In recognition of this limitation for determining occurrence, we used three levels of probability of occurrence (low, medium, and high) rather than using a definitive yes–no cutoff.

Errors in the ecological variables (drainage area, basin slope, reach slope, and reach elevation) are related to the resolution of the digital stream layer and accuracy of the DEM. A digital elevation model is a grid with elevations that represent the earth's surface. Raw DEM data typically contain erroneous features that prevent the downhill movement of water across the surface. A drainage enforcement function uses GIS smoothing algorithms to correct these erroneous cells by filling depressions and cropping barriers. The use of a 10 m drainage-enforced DEM improves the accuracy of watershed boundary identification over a 30 m DEM lacking drainage enforcement (Clarke and Burnett 2003). We used a 25 m DEM with drainage enforced.

Land-use variables were measured from a variety of sources. Percent harvest was measured from digital maps of cutover areas. We confirmed this information using digital orthophotographs. Percent harvest was intended to provide a surrogate indicator for changes in the hydrologic regime. However, hydrologic changes are not permanent and recovery occurs with forest regrowth. Road density was calculated using existing digital road information that was confirmed using digital orthophotos. Sediment inputs at a road crossing are related to characteristics of the road surface and ditches (Brooks et al. 2006); however, such factors were not considered in our models. Our criteria for identifying potential migration barriers are consistent with policy recommendations for maintaining fish passage under the Canada Fisheries Act, and a portion of the potential barriers may be passable to certain species and life stages. Beaver dams, logjams, head cuts, and waterfalls are common natural migration barriers that are not mapped and thus were not included in our models. Despite these limitations, this information provides a valuable context for interpreting fish occurrence patterns.

## Results

### Sampling summary

Our study was limited to small streams with drainage areas of <20 km$^2$. Bankfull width for streams with drainage areas between 15 and 20 km$^2$ averaged 4.9 ± 1.5 m. The channel length correction factor (slope × 0.78) was applied to all GIS measures of reach slope for these streams. Based on this drainage area cutoff, sample sizes by project area were as follows: MW, 284; HR inventory, 542; BR inventory, 66. Prevalence of brook trout among these three project areas was as follows: MW, 7%; HR, 12%; BR, 0% (mean for brook trout present areas = 10%). Prevalence of bull trout was as follows: MW, 25%; HR, 8%; BR, 12% (mean = 15%). Prevalence of rainbow trout was as follows: MW, 50%; HR, 29%; BR, 32% (mean = 37%). Prevalence of one or more of any species was as follows: MW, 66%; HR, 43%; BR, 33% (mean = 47%). In addition to the three target species, 14 additional species were encountered as incidental catches and were also included in the "all species" model along with the three target species.

In the Pearson correlation test, mean basin slope was correlated with mean basin elevation and percent wetlands. The variables retained included area (A), mean basin slope + mean basin slope$^2$ (B), reach slope + reach slope$^2$ (S), and elevation (E). The eight models tested included A, A+B, A+S, A+E, A+B+S, A+B+E, A+S+E, and A+B+S+E.

Three of the four independent ecological variables shared similar means and standard deviations among the three projects. Drainage area averaged 7.4 km$^2$ (MW, 8.0 ± 5.0 km$^2$; HR, 6.2 ± 5.1 km$^2$; BR, 7.9 ± 5.8 km$^2$), reach slope averaged 2.7% (MW, 2.8% ± 1.8%; HR, 3.2% ± 2.8%; BR, 2.2% ± 1.6%), and elevation averaged 1250 m above sea level, ASL (MW, 1270 ± 150 m ASL; HR, 1290 ± 190 m ASL; BR, 1190 ± 230 m ASL). Although basin slope had averaged 13.2% between the projects, the mean values were from a broader range (MW, 18.2% ± 11.4%; HR, 12.6% ± 7.6%; BR, 8.9% ± 8.5%). Land-use variables were only measured for the monitoring watersheds project. Percent harvest averaged 20.1% (0.0%–97.6%), and road density averaged 0.34 km·km$^{-2}$ (0.0–2.54 km·km$^{-2}$). We inspected 302 crossings that intersected mapped streams, including those in intermittent watercourses. Average hang height of the culverts rated as potential barriers was 0.27 m. We identified downstream barriers at 25% of electrofished reaches.

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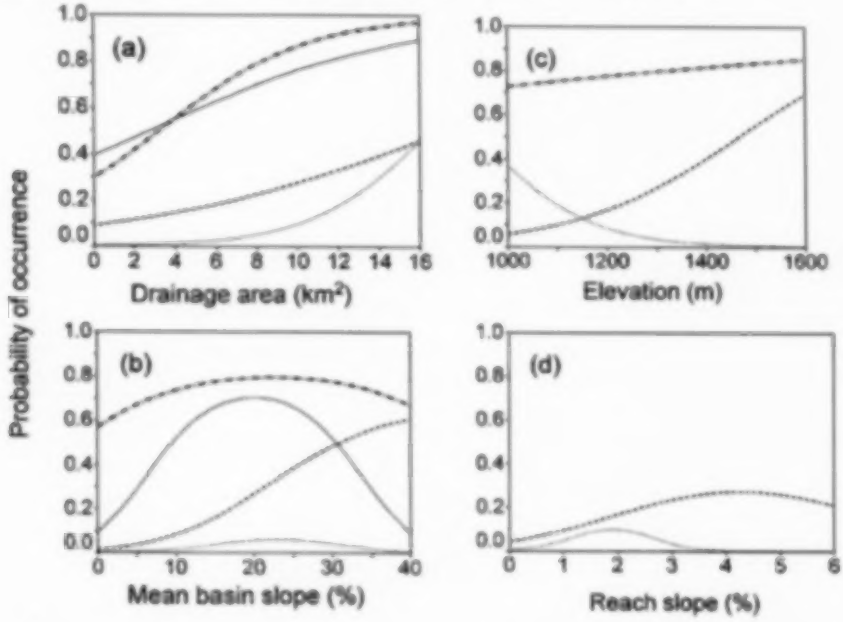
**Table 2.** Logistic regression models of ecological variables predicting the probability of occurrence of brook trout (*Salvelinus fontinalis*), bull trout (*Salvelinus confluentus*), rainbow trout (*Oncorhynchus mykiss*), and all species present.

| Species | Model name | $K$ | $AIC_c$ | $\Delta_i$ | $w_i$ | $p\hat{C}$ |
|---|---|---|---|---|---|---|
| Brook trout | Area + basin slope + elevation + reach slope | 7 | 100.34 | 0.00 | 0.45 | 0.97 |
| | Area + elevation + reach slope | 5 | 100.78 | 0.44 | 0.36 | 0.63 |
| | Area + basin slope + elevation | 5 | 102.72 | 2.38 | 0.14 | 0.88 |
| Bull trout | Area + basin slope + elevation + reach slope | 7 | 192.54 | 0.00 | 0.62 | 0.32 |
| | Area + basin slope + elevation | 5 | 193.57 | 1.03 | 0.37 | 0.10 |
| Rainbow trout | Area + basin slope | 4 | 267.45 | 0.00 | 0.55 | 0.69 |
| | Area + basin slope + elevation | 5 | 269.43 | 1.98 | 0.20 | 0.76 |
| | Area + basin slope + reach slope | 6 | 269.66 | 2.21 | 0.18 | 0.02 |
| All species | Area + basin slope | 4 | 246.86 | 0.00 | 0.35 | 0.08 |
| | Area + basin slope + elevation | 5 | 247.84 | 0.98 | 0.21 | 0.21 |
| | Area + basin slope + reach slope | 5 | 248.91 | 2.06 | 0.13 | 0.10 |
| | Area + elevation | 3 | 249.27 | 2.41 | 0.10 | 0.02 |

**Note:** $K$, the number of model parameters; $AIC_c$, the small sample version of Akaike's information criteria (AIC); $\Delta_i$, AIC difference between a given model and highest ranked model; $w_i$, Akaike model selection weights; and $p\hat{C}$, the Hosmer and Lemeshow goodness-of-fit chi-square.

**Fig. 2.** Predicted probability of occurrence by habitat variables for brook trout (*Salvelinus fontinalis*) (dotted line), bull trout (*Salvelinus confluentus*) (broken line), rainbow trout (*Oncorhynchus mykiss*) (solid line), and all fishes (dashed–dotted line): (*a*) drainage area, (*b*) mean basin slope, (*c*) elevation (m), and (*d*) reach slope. The range of the *x* axis represents the approximate observed range of each variable. For predictions, all values for other variables were standardized to mean values.




### Best ecological models

Based on the $AIC_c$ weights ($w_i$), global models for both brook trout and bull trout occurrence had the highest probability as the best model (Table 2). For the rainbow trout and "all species" models, there was less evidence for one best model. According to Burnham and Anderson (2002), an evidence ratio ($\Delta_i$) of less than 2.0 between models does not show strong support for any one model and they advise on choosing based on ecological–management sense. For rainbow trout, we selected the model with the highest $w_i$ as the best model. This model was the most parsimonious, and based on $p\hat{C}$, the model also fit the data well (Table 2). For all species, we selected the model with the second highest $w_i$ (area + basin slope + elevation) as the best ecological model. There was some evidence based on $p\hat{C}$ that the model with the highest $w_i$ did not fit the data, whereas there was no evidence that the second-ranked model did not fit the data (Table 2).

Under average conditions (i.e., basin slope and elevation), rainbow trout were more prevalent in smaller streams than bull trout and brook trout. Streams with a drainage area greater than 3 km$^2$ had a high probability of rainbow trout (cutoff = 0.51) (Fig. 2). The high probability threshold for both brook trout (cutoff = 0.08) and bull trout (cutoff = 0.25)

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**Table 3.** Classification analysis for high and medium predicted occurrence probability categories for best ecological models by species (brook trout (*Salvelinus fontinalis*), bull trout (*Salvelinus confluentus*), rainbow trout (*Oncorhynchus mykiss*), and all species).

| Species | Cutoff | Data set | *n* | Prevalence | AUC | PCC (1) | PCC (0) | PCC | Kappa |
|---|---|---|---|---|---|---|---|---|---|
| Brook trout | High (0.08) | Training | 238 | 9 | 0.92 | 81 | 82 | 82 | 0.36 |
| | | HR | 540 | 13 | 0.63 | 29 | 88 | 80 | 0.16 |
| | | Mean | | | 0.77 | 55 | 85 | 81 | 0.26 |
| | Medium (0.04) | Training | 238 | 9 | | 95 | 70 | 72 | 0.27 |
| | | HR | 540 | 13 | | 33 | 82 | 75 | 0.12 |
| | | Mean | | | | 64 | 76 | 74 | 0.19 |
| Bull trout | High (0.27) | Training | 238 | 25 | 0.88 | 77 | 79 | 78 | 0.49 |
| | | Testing | 46 | 22 | 0.69 | 60 | 72 | 70 | 0.27 |
| | | HR | 540 | 8 | 0.68 | 40 | 85 | 81 | 0.16 |
| | | BR | 66 | 12 | 0.96 | 63 | 97 | 92 | 0.62 |
| | | Mean | | | 0.80 | 60 | 83 | 80 | 0.39 |
| | Medium (0.13) | Training | 238 | 25 | | 92 | 60 | 68 | 0.38 |
| | | Testing | 46 | 22 | | 80 | 58 | 63 | 0.26 |
| | | HR | 540 | 8 | | 53 | 71 | 70 | 0.11 |
| | | BR | 66 | 12 | | 75 | 93 | 91 | 0.62 |
| | | Mean | | | | 75 | 71 | 73 | 0.34 |
| Rainbow trout | High (0.51) | Training | 238 | 50 | 0.79 | 71 | 73 | 72 | 0.45 |
| | | Testing | 46 | 52 | 0.78 | 67 | 73 | 70 | 0.39 |
| | | HR | 540 | 29 | 0.62 | 47 | 77 | 68 | 0.24 |
| | | BR | 66 | 32 | 0.81 | 57 | 87 | 77 | 0.46 |
| | | Mean | | | 0.75 | 61 | 77 | 72 | 0.38 |
| | Medium (0.25) | Training | 238 | 50 | | 93 | 39 | 66 | 0.32 |
| | | Testing | 46 | 52 | | 92 | 32 | 63 | 0.24 |
| | | HR | 540 | 29 | | 86 | 24 | 42 | 0.07 |
| | | BR | 66 | 32 | | 90 | 51 | 64 | 0.33 |
| | | Mean | | | | 90 | 36 | 59 | 0.24 |
| All species | High (0.63) | Training | 238 | 68 | 0.81 | 76 | 74 | 76 | 0.48 |
| | | Testing | 46 | 54 | 0.74 | 76 | 57 | 67 | 0.34 |
| | | HR | 540 | 43 | 0.69 | 58 | 75 | 68 | 0.34 |
| | | BR | 66 | 33 | 0.77 | 82 | 68 | 73 | 0.45 |
| | | Mean | | | 0.75 | 73 | 69 | 71 | 0.40 |
| | Medium (0.31) | Training | 238 | 68 | | 99 | 17 | 73 | 0.21 |
| | | Testing | 46 | 54 | | 100 | 14 | 61 | 0.15 |
| | | HR | 540 | 43 | | 92 | 15 | 49 | 0.07 |
| | | BR | 66 | 33 | | 91 | 41 | 58 | 0.25 |
| | | Mean | | | | 96 | 22 | 60 | 0.17 |

**Note:** High cutoff, the threshold of optimal sensitivity and specificity from ROC curve; medium cutoff, 0.5 × the high cutoff value; AUC, area under ROC curve; PCC (1), model sensitivity defined as percent of fish occurrence sites correctly classified; PCC (0), model specificity defined as percent of no fish occurrence sites correctly classified; PCC, overall prediction success.

was near 10 km$^2$. Different ecological niches among the three species were apparent from the predicted probabilities for basin slope and reach slope (Fig. 2). Maximum probability for brook trout, bull trout, and rainbow trout occurred in basins with average slopes of 16%–28%, 30%–40%, and 12%–28%, respectively. Bull trout probability increased with elevation, whereas brook trout displayed the opposite trend.

Model performance varied among species and data sets (Table 3). Based on average area under the ROC curve, all models had moderate performance at high cutoff values. Model sensitivity improved with lower cutoff values for all models. For rainbow trout and all species, sensitivity improved to high with reduced cutoff values. The use of the lower cutoff value resulted in reduced specificity, overall accuracy, and kappa. Based on kappa values, all models performed moderately at the high cutoff value, except for the brook trout model, which had a low performance rating. Performance of all models (based on area under ROC curve, sensitivity, and kappa) decreased with the HR inventory. Sixty percent of the incorrectly classified bull trout sites were located within 2 km of a stream with a drainage area >20 km$^2$.

## Predicted spatial distributions

The different niches for the three target species were also apparent from fish species distribution maps (Fig. 3). Brook trout had the greatest predicted extent within the streams originating in the lower foothills, whereas rainbow trout and bull trout had the greatest predicted extent within streams originating in the upper foothills and in the subalpine natural subregion, respectively.

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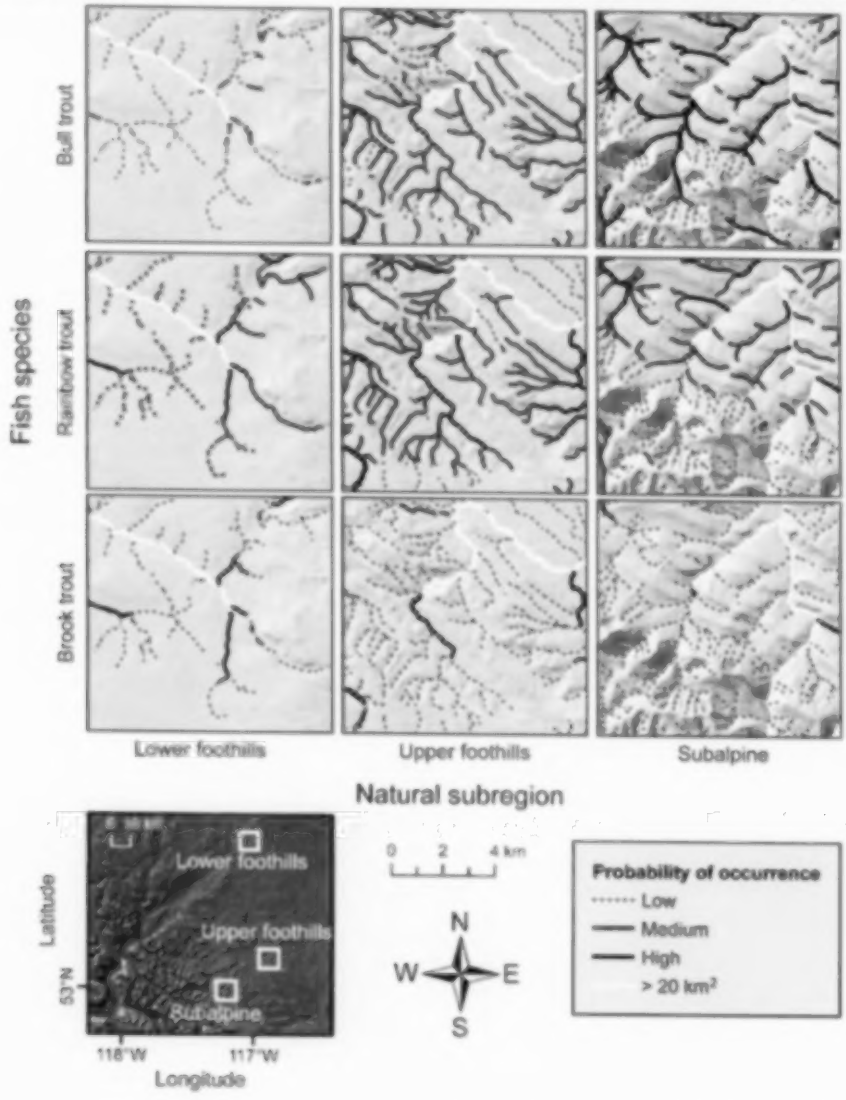
**Fig. 3.** Maps of predicted occurrence probability for bull trout (*Salvelinus confluentus*), rainbow trout (*Oncorhynchus mykiss*), and brook trout (*Salvelinus fontinalis*) within representative areas of the lower foothills, upper foothills, and subalpine natural subregions.




### Best ecological – land-use models

Underlying relationships between land-use variables and basin slope present a confounding factor to consider when interpreting correlations between land-use variables and fish occurrence (Fig. 4). All three land-use activities including harvest (H), road density (R), and downstream barrier (D) were limited to reaches with basin slopes <25%. The eight models tested included the best ecological model (E), E+H, E+R, E+D, E+H+R, E+H+D, E+R+D, and E+H+R+D.

The five top-ranked brook trout models shared a $\Delta_i < 2.0$, indicating little support for one best model (Table 4). In the highest ranked model, area had the greatest odds ratio, followed by harvest. The regression parameter values indicate a greater probability of capturing brook trout as harvest increases, but a lower probability as roads increase (Table 5). Percent harvest also had a low standard error. Road density had a high standard error and also included the value 1 within the odds ratio confidence interval to indicate "no effect" is within the interval. The kappa value indicates medium performance of the best ecological – land-use model, whereas the ecological model had a lower rating (Table 6). All other performance measures indicate similar trends.

The five top-ranked bull trout models shared a $\Delta_i < 2.0$, indicating little support for one best model (Table 4). The highest ranked model included downstream barriers as the only land-use variable. The ranking from largest odds ratio in this model was basin slope, elevation, and then drainage area (Table 5). One parameter in each quadratic term (i.e.,

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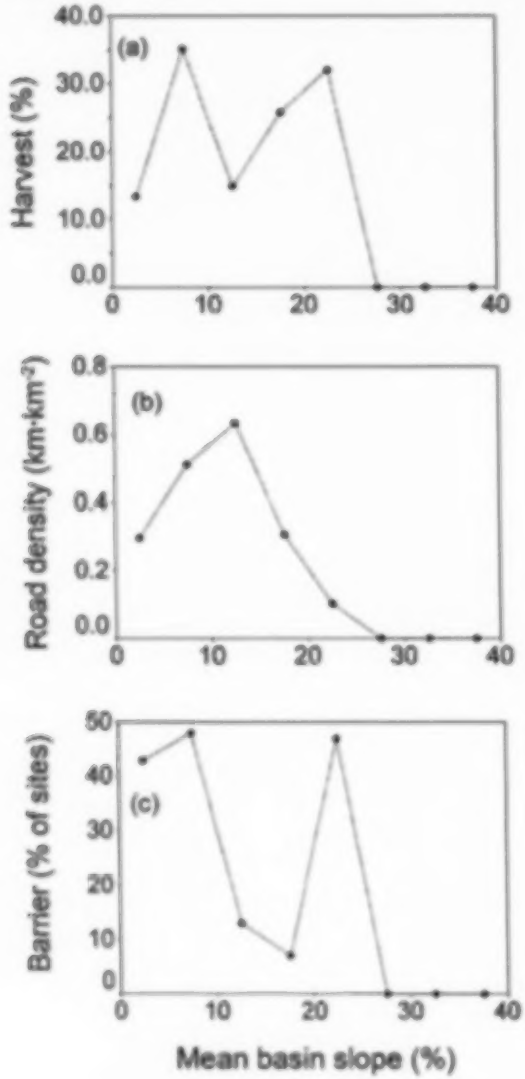
**Fig. 4.** Correlations between mean basin slope and land-use variables using bin-averaged values of each land-use variable with bins distinguished by a 5% step in mean basin slope: (*a*) percent of basin harvested, (*b*) road density, and (*c*) percent of sites with downstream barrier present.




basin slope$^2$ and reach slope) had high standard errors and included 1 within the confidence interval. The presence of a downstream barrier was associated with a reduction in odds by a factor of 0.274, and the odds ratio confidence interval did not include 1. The performance evaluation of the highest ranked model indicated improved performance over the ecological model (Table 6).

There was little evidence ($\Delta_i < 2.0$) for one best rainbow trout model (Table 4). Based on $pC$, the second-ranked model, which included harvest, fit the data well, whereas there was evidence that the model with the highest $w_i$ did not. Therefore we selected the model that included harvest as the only land-use variable as the best model. Harvest was associated with a negligible increase in odds, and the confidence interval did include 1 to indicate the potential of no effect (Table 5). Overall model performance decreased with the addition of the only plausible land-use variable into the best ecological model for rainbow trout (Table 6).

## Discussion

### Occurrence patterns of nonnative and native salmonids

Brook trout had higher probability of occurrence in larger, low-elevation channels. These findings were similar to those of another study in the Rocky Mountains where brook trout tended to persist in the main channels at lower elevations after dispersing from upstream stocking locations (Paul and Post 2001). In our study, brook trout occurrence increased in basins with higher harvest levels, and although other researchers have attributed these patterns to habitat degradation resulting from land-use activities, such relationships cannot be inferred within this study area. Timber harvest within riparian areas can cause habitat changes, including increased water temperature (MacDonald et al. 1990), and these changes may favor brook trout over bull trout (Selong et al. 2001) and native cutthroat trout (*Oncorhynchus clarki clarki*) (Shepard 2004). However, timber-harvesting practices in the study area have always included retention of streamside buffers. Furthermore, land-use activities were most prevalent in the intermediate relief basins that brook trout commonly inhabited and largely absent in higher-relief areas where brook trout were less frequently encountered. Alternate explanations include brook trout stocking at stream crossings rather than habitat modification.

The best ecological model for bull trout performed moderately. A logistic regression model for bull trout occurrence from a nearby foothills watershed had a similar ROC value (0.80); however, it included field measures (stream width and percent fines) combined with GIS measures of stream slope and harvest (Ripley et al. 2005). They found increased bull trout occurrence with increased stream width and reduced occurrence as percent fines, stream slope, and harvest levels increased. In contrast, we found a nonlinear relationship with stream slope and little evidence for including percent harvest in our best overall model. Our model also indicated a nonlinear relationship with basin slope tending towards steeper terrain and an increase in occurrence with increased elevation. Our best model included the downstream barrier as a land-use variable, and this contributed to an improvement in the ROC score from 0.78 to 0.81. All of the sample reaches with barriers had basin slopes <25%, which is below the optimal relief for bull trout. Although there may be some potential for a confounding effect from the exclusive occurrences of bull trout and this land-use variable, we did capture bull trout immediately below an impassible railway crossing in Pinto Creek, but not in any of the upstream tributaries. Similar patterns were observed in Japan where extinction rates of white-spotted char (*Salvelinus leucomaenis*) upstream from dams increased at a greater rate in headwater streams than in downstream areas (Morita and Yamamoto 2002).

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**Table 4.** Logistic regression models of ecological and land-use variables predicting the probability of occurrence of brook trout (*Salvelinus fontinalis*), bull trout (*Salvelinus confluentus*), and rainbow trout (*Oncorhynchus mykiss*).

| Species | Model name | $K$ | $AIC_c$ | $\Delta_i$ | $w_i$ | $pC^2$ |
|---|---|---|---|---|---|---|
| Brook trout | Ecological, harvest, roads | 9 | 93.29 | 0.00 | 0.37 | 0.18 |
| | Ecological, harvest | 8 | 93.51 | 0.22 | 0.33 | 0.51 |
| | Ecological, harvest, barrier | 9 | 95.37 | 2.08 | 0.13 | 0.79 |
| | Global | 10 | 95.45 | 2.16 | 0.13 | 0.19 |
| Bull trout | Ecological, barrier | 8 | 188.57 | 0.00 | 0.26 | 0.82 |
| | Ecological, harvest, barrier | 9 | 189.20 | 0.63 | 0.19 | 0.91 |
| | Ecological, roads, barrier | 9 | 189.79 | 1.22 | 0.14 | 0.99 |
| | Ecological, harvest | 8 | 189.89 | 1.32 | 0.14 | 0.21 |
| | Global | 10 | 190.36 | 1.79 | 0.11 | 0.93 |
| | Ecological, harvest, roads | 9 | 190.74 | 2.17 | 0.09 | 0.38 |
| Rainbow trout | Ecological, harvest, roads | 6 | 265.85 | 0.00 | 0.25 | 0.00 |
| | Ecological, harvest | 5 | 266.29 | 0.43 | 0.20 | 0.56 |
| | Ecological, roads | 5 | 266.78 | 0.93 | 0.16 | 0.34 |
| | Ecological | 4 | 267.45 | 1.60 | 0.11 | 0.69 |
| | Global | 7 | 267.97 | 2.12 | 0.09 | 0.04 |
| | Ecological, roads, barrier | 6 | 268.28 | 2.43 | 0.07 | 0.37 |
| | Ecological, harvest, barrier | 6 | 268.34 | 2.48 | 0.07 | 0.36 |

**Note:** $K$, the number of model parameters; $AIC_c$, the small sample version of Akaike's information criteria ($AIC$); $\Delta_i$, AIC difference between a given model and highest ranked model; $w_i$, Akaike model selection weights; and $pC^2$, the Hosmer and Lemeshow goodness-of-fit chi-square.

**Table 5.** Logistic regression parameter estimates from the best ecological – land-use models for each of three fish species (brook trout (*Salvelinus fontinalis*), bull trout (*Salvelinus confluentus*), rainbow trout (*Oncorhynchus mykiss*)) and all species present, including standard error of the model coefficient (SE), odds ratio, and associated lower and upper 95% confidence intervals (CIs).

| | | | | | 95% CIs | |
|---|---|---|---|---|---|---|
| Model | Parameter | Estimate | SE | Odds ratio | Lower | Upper |
| Brook trout | Area | 1.763 | 0.421 | 5.827 | 2.554 | 13.294 |
| | Basin slope | 0.606 | 0.807 | 1.833 | 0.377 | 8.920 |
| | Basin slope$^2$ | –1.234 | 0.813 | 0.291 | 0.059 | 1.434 |
| | Reach slope | –2.522 | 1.712 | 0.080 | 0.003 | 2.301 |
| | Reach slope$^2$ | –2.924 | 1.533 | 0.054 | 0.003 | 1.083 |
| | Elevation | –2.088 | 0.713 | 0.124 | 0.031 | 0.501 |
| | Percent harvest | 1.419 | 0.501 | 4.132 | 1.548 | 11.031 |
| | Road density | –0.949 | 0.707 | 0.387 | 0.097 | 1.547 |
| | Constant | –3.557 | 0.782 | 0.029 | | |
| Bull trout | Area | 0.703 | 0.260 | 2.019 | 1.212 | 3.363 |
| | Basin slope | 1.442 | 0.474 | 4.230 | 1.672 | 10.701 |
| | Basin slope$^2$ | –0.326 | 0.186 | 0.722 | 0.502 | 1.039 |
| | Reach slope | 0.647 | 0.380 | 1.911 | 0.907 | 4.025 |
| | Reach slope$^2$ | –0.385 | 0.182 | 0.680 | 0.476 | 0.972 |
| | Elevation | 0.908 | 0.296 | 2.480 | 1.388 | 4.432 |
| | Barrier downstream | –1.295 | 0.570 | 0.274 | 0.090 | 0.836 |
| | Constant | –0.906 | 0.309 | 0.404 | | |
| Rainbow trout | Area | 0.751 | 0.173 | 2.120 | 1.511 | 2.974 |
| | Basin slope | 0.434 | 0.228 | 1.544 | 0.988 | 2.413 |
| | Basin slope$^2$ | –0.989 | 0.192 | 0.372 | 0.255 | 0.542 |
| | Percent harvest | 0.011 | 0.006 | 1.011 | 0.999 | 1.023 |
| | Constant | 0.621 | 0.241 | 1.861 | | |

**Note:** To assist in interpretation of regression coefficients, all independent variables, except the categorical variable "barrier downstream", were scaled to standardized scores.

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**Table 6.** Classification analysis for high occurrence category for best ecological – land-use models by species (brook trout (*Salvelinus fontinalis*), bull trout (*Salvelinus confluentus*), rainbow trout (*Oncorhynchus mykiss*)).

| Species | Model | Cutoff | Data set | *n* | Prevalence | AUC | PCC (1) | PCC (0) | PCC | Kappa |
|---|---|---|---|---|---|---|---|---|---|---|
| Brook trout | Ecological | 0.08 | Training | 238 | 9 | 0.922 | 81 | 82 | 82 | 0.359 |
| | Ecological, harvest, roads | 0.09 | Training | 238 | 9 | 0.94 | 86 | 86 | 86 | 0.455 |
| Bull trout | Ecological | 0.27 | Training | 238 | 25 | 0.883 | 77 | 79 | 78 | 0.488 |
| | | | Testing | 46 | 22 | 0.685 | 60 | 72 | 70 | 0.265 |
| | | | Mean | | | 0.784 | 68 | 75 | 74 | 0.377 |
| | Ecological, barriers | 0.31 | Training | 238 | 25 | 0.889 | 82 | 84 | 83 | 0.595 |
| | | | Testing | 46 | 22 | 0.732 | 60 | 69 | 67 | 0.235 |
| | | | Mean | | | 0.811 | 71 | 77 | 75 | 0.415 |
| Rainbow trout | Ecological | 0.51 | Training | 238 | 50 | 0.793 | 71 | 73 | 72 | 0.445 |
| | | | Testing | 46 | 52 | 0.777 | 67 | 73 | 70 | 0.392 |
| | | | Mean | | | 0.785 | 69 | 73 | 71 | 0.419 |
| | Ecological, harvest | 0.51 | Training | 238 | 50 | 0.795 | 71 | 72 | 72 | 0.437 |
| | | | Testing | 46 | 52 | 0.714 | 67 | 59 | 63 | 0.258 |
| | | | Mean | | | 0.756 | 69 | 66 | 67 | 0.348 |

**Note:** Cutoff, the threshold of optimal sensitivity and specificity from ROC curve; AUC, area under ROC curve; PCC (1), model sensitivity defined as percent of fish occurrence sites correctly classified; PCC (0), model specificity defined as percent of no fish occurrence sites correctly classified; PCC, overall prediction success.

The high odds ratio for basin slope illustrates a strong relation with bull trout occurrence. Basin slope was positively correlated with mean basin elevation, a climatic descriptor, and negatively correlated with percent wetlands, a terrain indicator. This variable has not been included as a candidate variable in other watershed-scale models of bull trout distribution (Paul and Post 2001; Ripley et al. 2005), but a similar variable was incorporated into other watershed-scale models of fish occurrence (Porter et al. 2000).

The use of reach elevation as a surrogate for climate proved successful in a bull trout model within the Rocky Mountains (Paul and Post 2001). Improvements to the climatic variable could capture the variations in water temperature due to groundwater inputs in intermediate relief areas. For example, mean summer temperature (June–September) in a study area stream that supports juvenile bull trout averaged 5.4 °C, whereas the mean temperature at a site in a similar adjacent watershed that does not typically support juvenile bull trout averaged 8.1 °C. These differences were attributed to different groundwater inputs between basins (Jablonski 1980). A number of reaches shared medium or high probability of bull trout and brook trout, including an important bull trout spawning stream. Knowledge of such locations where the two species overlap is important for identifying where threats to bull trout persistence occur (Rieman et al. 2006). Therefore, future efforts to model bull trout occurrence should include the locations of groundwater upwelling areas, especially within lower-elevation streams that may otherwise provide marginal bull trout habitat.

The differences between our findings and those of another correlative investigation into bull trout occurrence in the foothills (Ripley et al. 2005) emphasize the need for process-based approaches that consider the confounding relationship between land use and basin relief. Bull trout are vulnerable to a range of human impacts including illegal angler harvest, disruption of migration at stream crossings and dams, loss of habitat productivity due to sedimentation, and increases in water temperatures. To support effective conservation efforts, future investigations should endeavor to rank these impacts.

In comparison to bull trout, rainbow trout occurred more frequently in reaches that also supported brook trout, and rainbow trout were more common in watersheds that supported high levels of land use. Rainbow trout tended towards small streams that were located in intermediate-relief terrain ideal for timber production and were less prevalent in lower-relief areas that support extensive muskegs. We observed that muskeg streams had sinuous channels, but these low-gradient reaches often lacked important rainbow trout habitat attributes including gravel substrate and pools. Given these observations, we were surprised that reach slope was not indicated within the best rainbow trout model. This absence of reach slope from the model has two divergent explanations. One previous study found no indication that trout populations were negatively affected by increases in stream slope (Isaak and Hubert 2000). However, two studies found that channel gradient constrained the upstream extent of coastal cutthroat and rainbow trout (Latterell et al. 2003; Fransen et al. 2006). We suggest the use of higher-resolution DEM data in future studies that explore the relationships between rainbow trout occurrence and stream slope. There are also important considerations when interpreting the suggested positive relationship between rainbow trout occurrence and land use. Our findings were similar to those for winter steelhead (*Oncorhynchus mykiss*) in Oregon where the proportion of watershed converted to shrub and young forest was positively related to winter steelhead redd abundance (Steel et al. 2004). This relation may be confounded by a strong affinity that this fish species may have for streams located within terrain well suited for land use. Also consider that contrary to our findings, one long-term study within our study area found that rainbow trout fry densities decreased after harvest when water yield exceeded a critical flow during the incubation period (Sterling 1992). Additional processed-based in-

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vestigations are required to identify land-use activities that may negatively decrease survival and growth rates of native rainbow trout across their range.

The "all species" model performed moderately well for predicting fish occurrence among all data sets. These results support the use of the "all species" model as a tool for fish habitat conservation efforts in the study area. Maintaining and restoring connectivity between streams is a cornerstone of most fish conservation strategies and also a legal requirement under the Canada Fisheries Act. Twenty-four percent of the 302 stream crossings were identified as potential migration barriers within medium or high probability streams. Culvert owners could complete a simple GIS exercise to determine the extent of potential fish habitat upstream of each crossing and use this information to identify infrastructure maintenance priorities or identify sites requiring additional inventories.

### Limitations and opportunities for modeling fish occurrence using remote methods

We identified a number of considerations for related efforts in the future. First, correlative investigations that quantify fish occurrence from multiple predictor variables are popular approaches used to improve our knowledge of factors affecting fish occurrence; however, they have limitations introduced by nonlinear relationships and nonmeasured correlates (Rosenfeld 2003). Furthermore, unlike mechanistic models and true experiments, these descriptive approaches cannot indicate cause–effect relations. Nonlinear relationships between a species and features of its environment are expected where a species is adapted to a specific ecological niche. These relations have been identified using artificial neural networks (Oakes et al. 2005) or by including a quadratic term within a logistic regression approach (Mattingly and Galat 2002). We selected the latter approach, which proved useful for indicating habitat partitioning among the target species in headwater streams. However, the Pearson correlation test was not well suited for identifying relationships between nonlinear variables. We identified such relationships by plotting predictor variables of interest.

Second, the accuracy of remote-sensed parameters may limit the interpretations of true habitat preferences, particularly for channel slope, which can provide an indication of expected channel unit distribution, including pool extent and frequency. We found that channel sinuosity in small streams is not accurately mapped, and meandering channels extended beyond commonly accepted gradient thresholds of between 2% and 4% (Church 1992). Sinuosity has an important effect on fish habitat because it decreases stream power by reducing stream slope and increasing form roughness within habitat elements, including undercut banks and pools (Leopold et al. 1964). Therefore, fish habitat characteristics are expected to vary between a straight channel with a 3% slope and a meandering channel with 3% slope. In watershed science, there is a trend to use streams automatically generated from high-resolution DEMs rather than air photo interpreted streams (Benda et al. 2007). Generated streams follow the path from one grid cell in the DEM to the lowest adjacent grid cell. However, line length reduction will remain a factor for these generated streams when the size of the watercourse is smaller than the grid-cell size.

Third, the bull trout model could be improved by incorporating additional variables including measures of the size of downstream habitats such as the Strahler order downstream of the next confluence (Oakes et al. 2005), the locations of natural migration barriers in downstream areas (Fransen et al. 2006), and variables that characterize temperature preferenda (Dunham et al. 2003), including indicators of groundwater upwelling areas (Baxter and Hauer 2000).

Fourth, scaling issues are a key component of resource selection function models (Boyce 2006). Future studies on relations between bull trout distribution and land use should address scaling. Ripley et al. (2005) included reaches with areas up to 374 $km^2$, whereas we limited our study to reaches with a drainage area of ≤20 $km^2$. We used this approach because we anticipated that correlations with land use would be more pronounced because of close linkages between aquatic habitat and terrestrial environment in small channels. However, study designs that include large streams may be more suited to addressing impacts from angling. Our automated procedure is well suited to scaling up from the reach scale to major watersheds >1000 $km^2$ where resource management strategies are applied. This ability to align a habitat model with the scale suitable to support resource management decisions can increase the utility of models in conservation and management programs (Boyce 2006).

In conclusion, an automated approach for modelling spatial fish occurrence patterns provides new insight into fish habitat requirements in small foothills streams. The approach is conducive to validation with external data sets. Fundamentally, the maps also provide an opportunity for biologists to visually compare their own inherent spatial models of fish occurrence with those developed mathematically and then to generate ideas on how to further improve our understanding of the factors affecting fish distribution.

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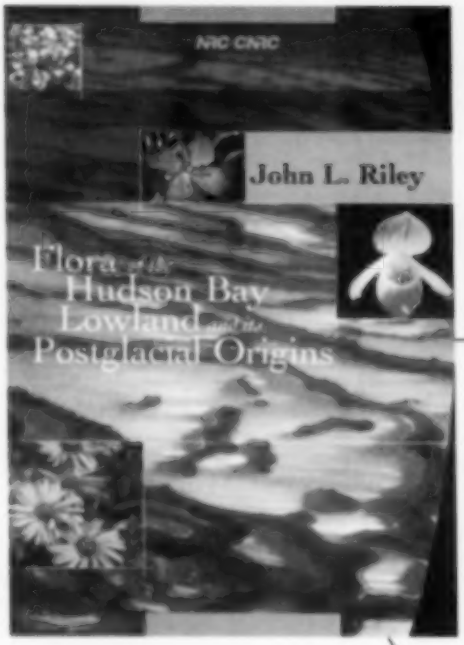


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